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THE MORPHOLOGY AND SYSTEMATICS OF SOME CRETACEOUS CRIBRIMORPH POLYZOA (PELMATOPORINAE)

G. P. LARWOOD

12 JUN 1962

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BY

GILBERT POWELL LARWOOD

12 JUN 62

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THE MORPHOLOGY AND SYSTEMATICS OF SOME CRETACEOUS CRIBRIMORPH POLYZOA (PELMATOPORINAE)

By G. P. LARWOOD

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SYNOPSIS

Ten genera of Cretaceous cribrimorph Polyzoa, previously described by Lang, are considered to belong to the Pelmatoporinae. Some of these genera, and numerous species, are regarded as synonymous and all are diagnosed and revised. Seven new species are diagnosed and described.

The morphology of Cretaceous cribrimorph Polyzoa is discussed and comparison made with Recent genera. Stratigraphical subdivisions of the English Chalk are reviewed and the distribution of the specimens from foreign Upper Cretaceous horizons is given. The stratigraphical range of the revised genera and species is described and their probable evolution reviewed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

SINCE the two catalogues on the Cretaceous cribrimorph Polyzoa by Dr. W. D. Lang were published in 1921 and 1922, the British Museum (Natural History) has received two very large collections of Chalk Polyzoa from Mr. C. T. A. Gaster. This has given the opportunity to examine and revise some of those results in the light of this added material, to re-assess the value of the cribrimorph Polyzoa as stratigraphical indices, and to reconsider the evidence for their evolution. It was found that, as in Recent cheilostomatous Polyzoa, there was much morphological variation in single species of the Cretaceous cribrimorphs, and far more in fact than Lang allowed for. As a result, many of his systematic subdivisions were found to be excessive.

The study of Cretaceous cribrimorph Polyzoa is made difficult by the complexity of their structure. Confusion has also arisen from the unique terminology introduced by Lang, and from his attempts to assign systematic and stratigraphical positions to species known only from earlier literature, where they were often poorly described and inadequately figured. Consequently I have not used Lang's terminology, but have used instead the more widely accepted terms which are generally applied to Recent and fossil Polyzoa. I have also rejected, as of uncertain systematic position, the ill-defined species just mentioned. Further, I have also rejected some of the hypothetical origins to which Lang attributed the development of certain structures, to which he gave evolutional significance, but to which the evidence appears opposed.

All this has led to a general reduction in the number of genera and species recognized, to a revision of their stratigraphical ranges, and to a great modification of the evolutionary sequences enunciated by Lang.

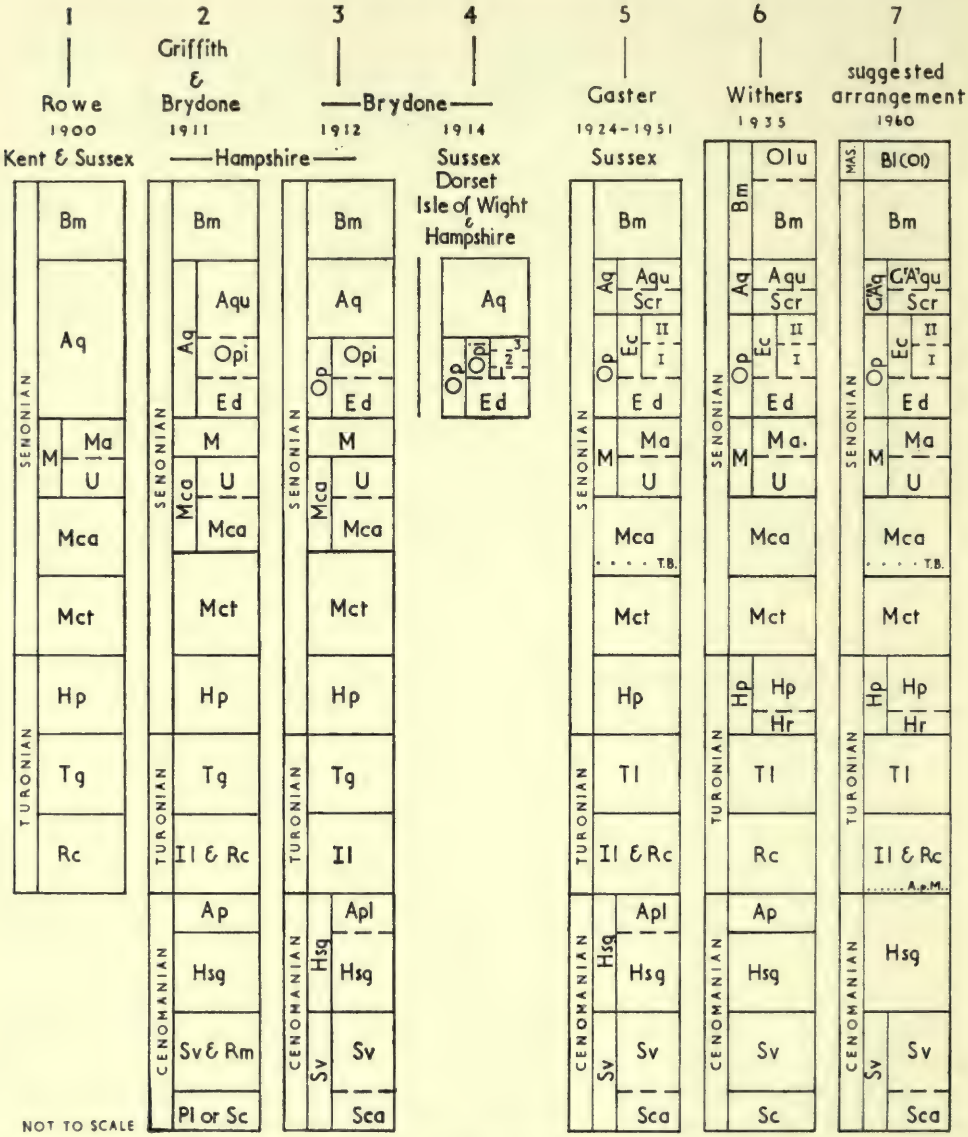
1
Rowe
1900
Kent & Sussex
2
Griffith & Brydone
1911
3
Brydone
1912
4
1914
Hampshire
Sussex Dorset Isle of Wight & Hampshire
5
Gaster
1924–1951
Sussex
6
Withers
1935
7
suggested arrangement
1960
SENONIAN
TURONIAN
CENOMANIAN
MAS.
Bl(Ol)
Olu
Bm
Aq
Aqu
Scr
G[A]q
G[A]qu
Opi
Op
Ec
Ed
M
Ma
U
Mca
T.B.
Mct
Hp
Hr
Tg
Tl
Rc
Il & Rc
Il
A.p.M.
Ap
Apl
Hsg
Sv & Rm
Sv
Pl or Sc
Sca
Sc
NOT TO SCALE

FIG. 1. Key to the abbreviations :

Ap = zone of *Actinocamax plenus*.
Apl = subzone of *A. plenus*.
A.p.m. = *Actinocamax plenus* Marls.
Aq = zone of *Actinocamax quadratus*.
Aqu = subzone of *A. quadratus*.
G[A]pM = *Gonioteuthis* [*Actinocamax*] *plenus* Marls.
G[A]q = zone of *Gonioteuthis* [*A.*] *quadrata*.
G[A]qu = subzone of *G.* [*A.*] *quadrata*.
Bl(Ol) = zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk).
Bm = zone of *Belemnitella mucronata*.
Ec = subzone of *Echinocorys scutata* var. *cincta*.
Ed = subzone of *Echinocorys scutata* var. *depressula*.
Hp = zone of *Holaster planus*.
Hsg = zone of *Holaster subglobosus*.
Il = zone of *Inoceramus labiatus*.
M = zone of *Marsupites testudinarius*.
Ma = subzone of *M. testudinarius*.
MAS = Maastrichtian Stage.

By using modern binocular microscopes I have been able to study structures in the Cretaceous cribrimorph Polyzoa which must have been invisible to Lang or less well defined with the instruments available to him. I wish to record my high appreciation of the great value of the work done by Lang in his extensive studies of this group of Cretaceous Polyzoa.

The present work[1] has been almost wholly carried out in the British Museum (Natural History) and my thanks are due to the Keepers of Palaeontology and Zoology for the facilities provided for my researches.

I wish to record particularly my warm appreciation of the considerable assistance given to me by Dr. Anna B. Hastings and Dr. H. Dighton Thomas to whom I am indebted for their invaluable advice, interest, suggestions and criticisms. I am also much indebted to Dr. H. Dighton Thomas for reading a large part of my typescript. I also wish to acknowledge the help of the library staffs at the British Museum (Natural History) and to thank Miss P. L. Cook and Mr. R. F. Wise for their general assistance, Mr. M. G. Sawyers for the photography and Miss C. M. P. von Hayeck and Mr. A. C. Townsend for preparing translations.

I am most grateful to Dr. J. F. Kirkaldy, Queen Mary College, University of London, for his supervision of my studies and for the criticisms he has given during the course of my work.

My gratitude is also due to Mr. A. G. Brighton, Curator of the Sedgwick Museum, Cambridge, for the loan of material and for information on the R. M. Brydone Collection ; to Mr. R. R. Clarke, Curator of Norwich Castle Museum, for the loan of material ; to Mons. E. Buge, of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, for photographs of, and information on, specimens from the d'Orbigny Collection and to the Editor of the *Bulletin of the Zoological Society of France* for permission to reproduce Plate 22, figs. 1–8.

Finally, I record my gratitude to my wife for help and encouragement with many problems associated with this work.

II. GENERAL STRATIGRAPHY

Subdivisions of the English Chalk which have been established or adopted by previous authors are discussed below. The subdivisions followed here (column 7, Text-fig. 1, p. 6) are based on a consideration of the extensive work of the authors mentioned.

[1] A major part of the subject of a thesis for the degree of Doctor of Philosophy in the University of London.

Mca = zone of *Micraster cor-anguinum*.
Mct = zone of *Micraster cortestudinarium*.
Olu = subzone of *Ostrea lunata*.
Op = zone of *Offaster pilula*.
Opi = subzone of *O. pilula*.
Pl = zone of *Plocoscyphia labrosa*.
Rc = zone of *Rhynchonella cuvieri*.
Rm = zone of *Rhynchonella martini*.
Sc = zone of *Stauronema carteri*.
Sca = subzone of *S. carteri*.
Scr = subzone of *Saccacoma cretacea*.
Sv = zone of *Schloenbachia varians*.
T.B. = *Trochiliopora Bed*.
Tg = zone of *Terebratulina gracilis*.
Tl = zone of *Terebratulina lata*.
U = subzone of *Uintacrinus westfalicus*.
1 = Lower belt of zone of *Offaster pilula*.
2 = Belt of *Echinocorys scutata* var. *cincta*.
3 = Upper belt of zone of *Offaster pilula*.
I = Horizon of *Hagenowia rostrata*.
II = Horizon of abundant *Offaster pilula*.

The *Ostrea lunata* Chalk is contained well within the zone of *Belemnella lanceolata* and is Maastrichtian in age. Gaster's (1924–51) main subdivisions of the zones of *Gonioteuthis* [*Actinocamax*] *quadrata* and *Offaster pilula* are followed, but Brydone's (1912) upward extension of the zone of *Micraster cor-anguinum* to include the *Uintacrinus* Chalk (usually placed in the zone of *Marsupites testudinarius*) has not been generally accepted and is not followed here.

SUBDIVISIONS OF THE ENGLISH CHALK

CENOMANIAN

Zone of *Schloenbachia varians*

The glauconitic, sandy marl, usually about one foot thick, which occurs at the base of this zone over much of southern England is here termed the subzone of *Stauronema carteri*; this agrees with Brydone's and Gaster's general use of the term. Griffith & Brydone (1911) and Withers (1935) gave the unit zonal status; it is not, however, sufficiently widespread or thick enough to be regarded as a true zone. Griffith & Brydone (1911) also suggested *Plocoscyphia labrosa* as an alternative name form, but apparently this sponge is only locally significant.

The Chalk Marl, with the Totternhoe Stone at the top, succeeds the *Stauronema carteri* subzone giving a general thickness of about 160 ft. for the zone of *Schloenbachia varians*. The thickness may be much less; at Hunstanton, Norfolk, it is only 18–20 ft. The zone of *Schloenbachia varians*, as determined for southern England, is not recognized in the Chalk of Lincolnshire and Yorkshire. Bower & Farmery's (1910) division of the Lincolnshire Cenomanian was adopted for that of Yorkshire by C. W. & E. V. Wright (1942). They divided the stage into a lower zone of *Holaster subglobosus* and an upper zone of *H. trecensis*, and estimated an inland thickness of 70 ft. for the whole stage.

Zone of *Holaster subglobosus*

In southern England this zone has a general thickness of about 100 ft. Griffith & Brydone (1911) and Withers (1935) excluded from it the *Actinocamax plenus* Marls, which they regarded as a separate zone. Subsequently both Brydone and Gaster have described these Marls as a subzone of the *Holaster subglobosus* Zone. C. W. & E. V. Wright (1951 : 3, 4) also regarded the *Actinocamax plenus* Marls as a distinct subzone, but stated " Their cephalopod fauna is of Turonian affinities, and it therefore seems best to treat them as a subzone of the *Inoceramus labiatus* zone ". The Marls vary in thickness from a few to about 12 ft. and are here regarded only as a lithological marker of the base of the Turonian in some areas.

TURONIAN

Zone of *Inoceramus labiatus* and " *Rhynchonella* " *cuvieri*[1]

Both name forms occur commonly in the zone which is about 70–90 ft. thick in southern England. In Yorkshire the zone is very thin—only 11 ft. of gritty Chalk with broken *Inoceramus labiatus* shells is present. As mentioned above, the *Actinocamax plenus* Marls are a lithological marker of the base of the zone.

---

[1] Pettit (1954 : 29) placed the species in *Orbirhynchia*.

Zone of *Terebratulina lata*

Withers's (1935 : 54) estimate of the general thickness of this zone in southern England as about 160 ft. is probably a maximum. Dines and others (1954) recorded up to 140 ft. of *T. lata* Chalk in the Chatham district, Kent, and Wright (1947) estimated only 58 ft. for the zone in Dorset. In Yorkshire it is very much thicker (210 ft.).

Zone of *Holaster planus*

Although Brydone and Gaster excluded this zone from the Turonian (see below), it is generally regarded as the topmost zone of that stage.

The base of the zone of *H. planus* is often well marked by the Chalk Rock. This hard, somewhat nodular, glauconitic, yellowish limestone, which is about 6 ft. thick, contains a shallow water fauna with *Hyphantoceras reussianum*. In the localities where the actual rock band is not developed, the fauna, although somewhat modified, is often present. This basal bed of the *Holaster planus* Zone is distinguished as the *Hyphantoceras reussianum* Subzone (see Withers, 1935 : 55).

The zone is generally thin ; the maximum thickness given by Withers is about 60 ft., the minimum 14 ft. However, the zone thickens northwards, Dines and others (1954) recorded up to 70 ft. of *Holaster planus* Chalk in the Chatham area of Kent, Peake & Hancock (1961) estimate 75 ft. for the zone in north Norfolk and Rowe (1904 : 193) estimated 125 ft. as the thickness of the zone in Yorkshire.

Wright (1947 : 202) drew attention to " a 2-foot band near the base of the zone [in Dorset] crowded with the polyzoan *Bicavea rotaformis* Gregory ". This very restricted occurrence of *Bicavea* contrasts with that of *B. radiata* Gaster and *B. striata* Gaster which are distributed throughout the zone of *Gonioteuthis* [*Actinocamax*] *quadrata* in the Senonian.

SENONIAN

Zone of *Micraster cortestudinarium*

As mentioned above, Griffith & Brydone (1911), Brydone (1912) and Gaster (1924–51) placed the base of the Senonian at the bottom of the *Holaster planus* Zone. The first two authors also regarded the lowest third of the generally accepted zone of *Micraster cor-anguinum* as the uppermost unit of the *Micraster cortestudinarium* Zone. Withers (1935 : 57) estimated a general thickness of about 60 ft. for the *M. cortestudinarium* Chalk.

Zone of *Micraster cor-anguinum*

Griffith & Brydone (1911) and Brydone (1912) placed the lower boundary of this zone about 85 ft. above the generally accepted level (e.g., Rowe, 1900), and raised the upper boundary by about 60 ft. to include the *Uintacrinus* Chalk ; this arrangement has not been adopted by later authors.

Peake & Hancock (1961) record 170 ft. of *M. cor-anguinum* chalk in Norfolk.

The upper boundary of the zone, as commonly defined at present, is the base of the *Uintacrinus* Chalk, its lower limit being placed about 260 ft. below that level.

Gaster (1920 : 526) first drew attention to the *Trochiliopora* Bed near the base of the zone of *Micraster cor-anguinum* in Sussex. He stated " the exact position in which it occurs . . . is as follows :

" Lower fourth of zone of *Micraster coranguinum*	Strong *M. coranguinum* tabular flint band. Chalk, about 35 feet. Chalk with *Trochiliopora* sp., 10 feet. Chalk, about 17 feet.

" Chalk of zone of *Micraster cortestudinarium* ".

This distinctive horizon in Sussex was not mentioned by Wright (1947) as recognizable in the Chalk of the *M. cor-anguinum* Zone of Dorset.

The " strong *Micraster cor-anguinum* tabular [flint band] " of Rowe (1900 : 301) was mentioned previously by Whitaker (1872 : 50). In his work on the Sussex Chalk Gaster (e.g., 1937 : 361) also recognized this marker flint band near the base of the zone. C. W. & E. V. Wright (1942) adopted, for Yorkshire, Rowe's (1904) suggestion of a zone of *Hagenowia rostrata* which is abundant throughout Chalk equivalent to the *Micraster cor-anguinum* Zone in southern England.

Zone of *Marsupites testudinarius*

This zone, about 125 ft. thick, has been recognized generally, e.g., Rowe (1900), Gaster (1924–51), Withers (1935) as comprising two " bands " or subzones—that of *Marsupites testudinarius* above (65 ft. thick) and that of *Uintacrinus westphalicus* below (60 ft. thick). As mentioned, Griffith & Brydone (1911) and Brydone (1912) did not include the *Uintacrinus* Chalk in their zone of *Marsupites testudinarius*. C. W. & E. V. Wright (1942 : 118) pointed out that Brydone's scheme avoids the anomaly of a " *Marsupites* Zone in one subzone of which *Marsupites* does not occur ". In the case of the Yorkshire Chalk they recognized a zone of *Uintacrinus* as have Peake and Hancock (1961) in Norfolk.

Brydone (1915 : 13–15) added a few feet of Chalk, containing unusual crinoid plates, to the top of the *Marsupites* Zone ; this change was also adopted by Gaster (1937 : 362).

Withers (1935 : 58) stated that " The *Marsupites* zone probably represents the maximum depth attained during the whole of the English Cretaceous period ".

Zone of *Offaster pilula*[1]

This zone, proposed by Brydone (1912 : 14), was established originally in the Chalk of Hampshire and later traced by him in Norfolk, Suffolk, Sussex, Dorset and the Isle of Wight (see Brydone, 1914*a*, 1932*a*, *b*). Blackmore was able to trace the zone in Wiltshire, and other workers have established its presence throughout the rest of the English Chalk.

---

[1] The original spelling of the specific name " *pilula* " was " *pillula* ", as *Ananchytes pillula* Lamarck (1816 : 27). Brydone (1912 : 7, footnote) stated with reference to the spelling *pilula*, " this name was deliberately spelt thus in ' The Zones ' (Griffith & Brydone, 1911) in deference to Mr. Griffith's scruples as a classical scholar against countenancing the spelling ' *pillula* ' . . . ".

Brydone divided the zone into a lower subzone of *Echinocorys scutata* var. *depressula* and an upper subzone of *Offaster pilula*. The *depressula* Subzone was not modified by Gaster, but for Brydone's *Offaster pilula* Subzone he (1924 : 94) substituted " subzone of *Echinocorys scutata* var. *cincta* ". In this subzone Gaster included the 60 ft. of Chalk comprising his " horizon of *Hagenowia rostrata* " ; the remainder of the subzone below it he termed the " horizon of abundant *Offaster pilula* ", almost equivalent to the three " belts " of the " subzone of *Offaster pilula* " of Brydone (1914*a*).

Brydone (1912 ; 1914*a*) and particularly Gaster (1924 : 103–107 ; 1930 : 329 ; 1937 : 326) established a sequence of " belts " characterized by different varieties of *Echinocorys scutata*. These are not shown in columns 4 and 5 of Text-fig. 1 but are summarized in tabular form by Gaster as mentioned above. The thickness of the zone of *Offaster pilula* was estimated by Withers (1935 : 59) as about 160 ft.

In Yorkshire, Chalk equivalent to the combined zones of *Offaster pilula* and *Gonioteuthis* [*Actinocamax*] *quadrata*, is characterized by the zonal form *Inoceramus lingua* with, at the top of the zone, a subzone of *Scaphites binodosus* regarded as the equivalent of the *Gonioteuthis* [*Actinocamax*] *quadrata* Zone of south-east England (C. W. & E. V. Wright, 1942 ; 1951 : 4). Peake & Hancock (1961) have not established this zone in Norfolk.

Zone of *Gonioteuthis* [*Actinocamax*] *quadrata*

Rowe's (1900) zone of *A. quadratus* was divided by Griffith & Brydone (1911) into three subzones. In 1912 Brydone combined the two lower subzones as the zone of *Offaster pilula* and restricted the *Actinocamax quadratus* Zone to the Chalk between his new zone and the base of the *Belemnitella mucronata* Zone. He included at the base of his restricted zone of *Actinocamax quadratus* about 60 ft. of Chalk which, in Sussex, Gaster (1924 : 93) regarded as the uppermost part of the underlying zone of *Offaster pilula* [i.e., the horizon of *Hagenowia rostrata*]. Gaster's arrangement was disputed by Brydone (1939) who re-stated his earlier opinion that the boundary between the zones of *Offaster pilula* and *Actinocamax quadratus* should be placed at the top of his " *Planoconvexus* Bed ".

Gaster (1924 : 93) recognized a subzone of *Saccacoma cretacea* for the upper 125 ft. of his restricted zone of *Actinocamax quadratus* in Sussex. *Saccacoma cretacea* is not here regarded as a true subzonal form : the general thickness of the restricted zone of *Gonioteuthis* [*Actinocamax*] *quadrata* was given by Withers (1935 : 59) as about 150 ft., so that *Saccacoma cretacea* extends through most of the zone. Similarly, the polyzoan species *Bicavea radiata* Gaster and *B. striata* Gaster occur throughout the whole zone and are not confined to separate horizons within it.

Zone of *Belemnitella mucronata*

The varying opinions on the position of the upper boundary of this zone are mentioned in the discussion of the overlying *Ostrea lunata* Chalk.

Apart from the inclusion, by some authors, of the *O. lunata* Chalk (e.g., Withers, 1935 : 60), and the Parapachydiscan divisions proposed by Spath (1926), the zone of *Belemnitella mucronata* has not been generally subdivided.[1] The position of the lower boundary of the zone of *Belemnitella mucronata* as established, for example, by Rowe (1900), has not been queried.

Variations in thickness are very marked : in a general estimate Withers (1935 : 60) gave the thickness as 250 ft. (excluding the *Ostrea lunata* Chalk) in Norfolk, 70 ft. in Hampshire, 250 ft. in Dorset, and 475 ft. in the Isle of Wight. The thickness in Norfolk has been more accurately estimated by Peake & Hancock (1961) as 325 ft.

Uneven pre-Tertiary or recent erosion probably accounts for much of this variation, but the thickness which remains is great and more general subdivision would be of value.

MAASTRICHTIAN

Zone of *Belemnella lanceolata*

In his original publication on the stratigraphy and fauna of the Trimingham Chalk, Brydone (1900 : 11) concluded that " the great majority of forms ... which appear in this [faunal] list ... are characteristic of the Maastrichtian Stage on the Continent ". Subsequently, Brydone (1908*a*, *b*) described the Trimingham Chalk in detail. Since that date the Trimingham Chalk has been placed, by various authors, either as highest Senonian or as Maastrichtian in age.

Boswell (1929 : 406, 408A) recognized Jukes-Browne's (1904 : 5, 12) zone of *Ostrea lunata* and regarded it as comprising " higher beds than those of the *B. mucronata* zone ".

Withers (1935 : 40) discussed the limits of the " Maestrichtian and Upper Senonian (Campanian) " and some of the previous uses of the term " Maestrichtian ". He stated that it " was originally applied by Dumont . . . to include the Tuffeau de Maestricht as exposed at Maestricht, Holland, and [that] this term corresponds to the Dordonian of Coquand ". He also mentioned Haug's (1910) extension of the term Maastrichtian to include the " Maestrichtian (*s. str.*) and the zone of *B. mucronata* ", and Spath's (1926) modification which included with the Maastrichtian only " the uppermost part of the *B. mucronata* zone ".

Withers himself (1935 : 41) applied the term " Maestrichtian ... in its original sense to beds of the same age as the Tuffeau de Maestricht ", and retained as " Upper Senonian (Campanian) " the " Norwich Chalk ", the Skrivekridt of Denmark and the Schreibkreide of Rügen. The Chalk of Trimingham, Norfolk, he regarded (p. 60) as being " a little higher in the sequence of the *B. mucronata* zone ... than that occurring in the neighbourhood of Norwich."

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[1] Wright (1947) mentioned " Lower, Middle and Upper Divisions " of the *Belemnitella mucronata* Zone in Dorset, the Middle Division being characterized by distinctive asteroid remains. C. W. & E. V. Wright (1951) adopted, in a slightly modified form, Spencer's (1913 : 145) division of the " *mucronata* " Chalk into Upper, Middle and Lower zones. They stated (1951 : 3) that of these divisions, " the first [topmost] is now the zone of *Belemnella lanceolata*, and the other two are treated as subzones, as yet unnamed, of a restricted zone of *Belemnitella mucronata* ".

The " Maestrichtian " was suggested by Brydone (1938 : 16) as a " possible continental equivalent " of the " Trimingham General Chalk ", i.e., his upper division of the zone of *Ostrea lunata*.

More recently, Jeletzky (1951), in a comprehensive study of the use of the name Maastrichtian, considered that the Trimingham Chalk is of Lower Maastrichtian age, an opinion based largely on a study of the belemnite faunas of Trimingham and other Maastrichtian horizons on the Continent. The highest *Belemnitella mucronata* Chalk he regarded as that of the Norwich district, which he retained in the Senonian (see Jeletzky, 1951, table facing p. 208).

Jeletzky's interpretation of Dumont's (1849) use of the term Maastrichtian has been questioned by van der Heide (1954). He stated (p. 509) that Dumont " considered the Maastrichtian Chalk and its equivalents as belonging to his Système Maestrichtien : older beds were not included ". After a careful and detailed assessment of the evidence from Dumont's pre-1849 publications, his maps, and Mourlon's publication (1878) based on Dumont's notes and manuscripts (Dumont died in 1857), van der Heide concluded that " the Système Maestrichtian of Dumont (1849) *is equivalent to the Maastricht Chalk* " of the type locality only, and that the newer interpretations, which enlarge the Maastrichtian (e.g. Jeletzky, 1951) are incorrect. Finally, van der Heide stated (p. 511) " the only conclusion at which we can arrive at the moment is that a detailed study of the stratigraphy and palaeontology of the type area of the Maastrichtian is indispensable ".

It is desirable to establish, as van der Heide has done, the original meaning of a stratigraphical term, but this should not then preclude its use in a wider sense—provided that the extended use is also clearly defined.

Recently Jeletzky's enlarged use of the term Maastrichtian has been applied, with various modifications, by several continental authors. For example, Voigt (1951) has described polyzoan faunas of Lower and Upper Maastrichtian age from Holland and Germany ; the zone of *Belemnitella mucronata* being retained in the Upper Campanian. This is in agreement with the extensive work of Hiltermann & Koch (1950), Hiltermann (1952) and Wicher (1949, 1953*a*, 1953*b*) which has shown that the top part of the previously so-called " Upper Senonian " of Denmark, Germany and other areas, may be regarded as a widespread boreal facies of the Maastrichtian (*s. lato*) characterized by a distinctive foraminiferal fauna.

In a study of the foraminifera of the English Chalk Williams-Mitchell (1948) indicated that the foraminifera of the Trimingham Chalk differ considerably from those which characterize the underlying Senonian horizons. Barnard & Banner (1953 : 207) listed 24 species of arenaceous foraminifera which occur in the zone of *Belemnitella mucronata* ; of these, 6 are long-range forms occurring from the Cenomanian to the zone of *Ostrea lunata*, 5 range from the base of the zone of *Belemnitella mucronata* into the *Ostrea lunata* Chalk, and the remaining 13 species are all confined to the zone of *Belemnitella mucronata*, again indicating a change at the top of the latter zone.

A sample collected in 1954 from a foreshore exposure of white chalk with *Ostrea lunata*, just north of Mundesley, was prepared and examined for its foraminiferal content by the late Mr. A. G. Davis. In a letter (20th September, 1954) he wrote

" the foraminiferal content of this sample is quite unlike any from the zones below —which are much better known. I find the foraminifera fauna is characterized by some species of *Bolivina*, species much like *B. incrassata*, *B.* " *gigantea* " and *B. decussens*. There are also some arenaceous agglomerated forms—as also mentioned by Williams-Mitchell.

The species of *Bolivina* present in the sample are characteristic of the Maastrichtian of Hemmoor and Lüneburg. They are rare in the *mucronata* Zone, but do make an appearance and only become abundant higher up. They are abundant in the Mundesley sample.

Other foraminifera are present, but not abundant, and they are of long range. The well-known Chalk foraminifera, Nodosarids, *Globotruncana*, etc., do not seem to be present."

This evidence of a faunal change in the foraminifera is further supported by the distribution of species of *Castanopora* (see p. 274).

Boswell (1923) estimated the total thickness of the *Ostrea lunata* Chalk at about 110 ft., and this is confirmed by Peake & Hancock (1961 : 320) in their precise study of the Trimingham Chalk. The boundary between it and the underlying zone of *Belemnitella mucronata* has not been seen.

C. W. & E. V. Wright (1951 : 3) have stated that " *Ostrea lunata*, the fossil used by Jukes-Browne as an index for the uppermost zone of the Chalk (at Trimingham), is not entirely appropriate [as a zonal name form], as it does not occur at all in a large part of the Trimingham Chalk. Now that Jeletzky has shown that the vast majority of the Trimingham belemnites are *Belemnella lanceolata* (Schlotheim) and not *Belemnitella mucronata* the former species can appropriately be used as a zone fossil, as it is over most of northern Europe ". Thus the authors referred (1951 : 3) to a zone of *Belemnella lanceolata* as an alternative to " zone of *Ostrea lunata* ". They also used the terms " Upper " and " Lower Senonian " as stages embracing the zones of *Ostrea lunata* down to, and including, the zone of *Offaster pilula*, and from the zone of *Marsupites testudinarius* down to, and including, the zone of *Micraster cortestudinarium* respectively. They stated that the " Upper Senonian includes Campanian and Maastrichtian. Lower Senonian includes Coniacian and Santonian ".

Foreign Upper Cretaceous Horizons

Most of the Polyzoa described here are from the English Chalk, but a number of specimens from various horizons of the Upper Cretaceous abroad have also been examined in order to complete the systematic revision of some genera.

The following list of genera and species from such localities and horizons are included in the systematic revision of the Cretaceous cribrimorph Polyzoa described here. When no specimens are available, either in the collections of the British Museum (Natural History), or in the other collections studied, the species have been assessed from published works only. In these cases the name of the species is followed in the list by the reference to its original description [e.g., *Castanopora* [*Rhiniopora*] *labiata* (Levinsen) (1907 : 155, 156, 158, pl. opp. p. 160, fig. 1, 1*a*–*f*). Møen, Aalborg, Denmark. Lower Maastrichtian (as Senonian, zone of *Belemnitella mucronata*)]. Where specimens of species from foreign localities are available the name of the species is marked by an asterisk and is followed directly by its locality and horizon [e.g., **Castanopora glandulosa* Lang. Rügen. Probably boreal Maastrichtian (as Senonian, zone of *Belemnitella mucronata*)]. If a photograph only is available this is stated. Published records of the foreign occurrences of other species are also mentioned.

AEOLOPORA

Aeolopora nebulosa Lang. Also recorded by Voigt (1930 : 498, 542, 560, pl. 27, fig. 1) from Ifö, Sweden. " Mammillatensenon."

CASTANOPORA

Castanopora [*Rhiniopora*] *aviculosa* (Lang). Photograph only of the holotype. Maastrichtian, Maastricht, Limbourg, Holland.

**C. castanea* Lang. Rügen. Also recorded by Voigt (1930 : 513, 561, pl. 30, fig. 17) from the same locality and horizon. Probably boreal Maastrichtian [as Senonian, zone of *Belemnitella mucronata*].

**C. dibleyi* (Brydone). Also recorded by Voigt (1930 : 512, 561, pl. 30, fig. 18) from Rügen. Probably boreal Maastrichtian, and ? Voigt (1930 : 512, 561, pl. 30, fig. 20) as *Castanopora* sp. from Stafversvad, Schonen [as " Unteres Mukronatensenon "].

C. faujasi (von Hagenow) (1851 : 99, pl. 10, fig. 19*a*, *b*). Also recorded by Voigt (1930 : 511, pl. 31, fig. 2) as *Rhiniopora faujasi* (von Hagenow), Maastricht, Limbourg, Holland. Maastrichtian [as " Ob. Mukronatensenon "].

**C. glandulosa* Lang. Rügen. Probably boreal Maastrichtian [as Senonian, zone of *Belemnitella mucronata*].

C. guascoi (Ubaghs) (1865 : 51, pl. 2, figs. 3*a*–*c*). Valkenburg (Fauquemont), east of Maastricht, Limbourg, Holland. Maastrichtian. Also recorded by Voigt (1930 : 512, 561, pl. 31, fig. 1). Maastricht. Maastrichtian [as " Ob. Mukronatensenon "].

**C.* [*Rhiniopora*] *jurassica* (Gregory). Recorded incorrectly from Ranville, Normandy, France, as of Jurassic age. Very probably from Maastricht, Limbourg, Holland. Maastrichtian.

C. [*Rhiniopora*] *labiata* (Levinsen) (1907 : 155, 156, 158, pl. opp. p. 160, fig. 1, 1*a*–*f*) = *Cribrilina valida* Levinsen (1925 : 376, pl. 5, fig. 58*a*–*d*). Møen, Aalborg, Denmark. Lower Maastrichtian, [as Skrivekridt, Senonian, zone of *Belemnitella mucronata*].

**C. magnifica* (d'Orbigny). Holotype—photograph only, either from Sainte Colombe, Manche, France, or from Royan, Charente Inférieure, France. Both localities Maastrichtian. [As Senonian, zone of *Belemnitella mucronata*.] Includes *Rhiniopora aspera*, *R. asperula*, *R. cacus* and *R. horrida*. Recorded by Voigt (1930 : 511) from Rügen and Blauen Bergen, Roslau. Probably boreal Maastrichtian [as " Ob. Mukronatensenon "]. Also recorded by Illies (1953) from Hemmoor, near Hanover, Germany. Maastrichtian.

C. multicostata Voigt (1930 : 512, 561, pl. 30, fig. 19). Rügen. Probably boreal Maastrichtian [as " Ob. Mukronatensenon "].

C. [*Rhiniopora*] *spooneri* (Butler & Cheetham) (1958 : 1154, text-figs. 1, 2). "... from a chalk bed exposed at Rayburn's dome, Bienville Parish, Lousiana ... equivalent to the Upper Cretaceous Saratoga chalk of Arkansas ..." U.S.A.

C. voigti sp. nov. (Voigt, 1930 : 511, pl. 31, fig. 6—as " *Rhiniopora hispida* Lang " which is indeterminate, see p. 238). Møen. Denmark. Lower Maastrichtian [as Oberes Mukronatensenon], and Rügen, probably boreal Maastrichtian.

HEXACANTHOPORA

**Hexacanthopora sexspinosa* Lang. Also recorded by Voigt (1930 : 495, 542, 560, pl. 26, figs. 11, 12) from " Gr. Bülten-Granulatensenon " (as *H. brightonensis*) and " Quadraten- oder Mukronatensenon " of Misburg, Germany.

H. viginticostata Voigt (1930 : 495, 560, pl. 26, fig. 13 ; 1949 : 37, 43, pl. 9, figs. 1, 2). Schwiecheldt, Hanover, Germany. " Quadraten- oder Mukronatensenon ", and Lägerdorf, Holstein, Germany, Senonian, zone of *Gonioteuthis* [*Actinocamax*] *quadrata.*

LAGYNOPORA

**Lagynopora furcifera* (Brydone). Also recorded by Voigt (1930 : 495, 542, 560, pl. 26, fig. 10 ; 1949 : 36, 43, 44, pl. 11, fig. 1). Misburg, Germany—" Quadraten- oder Mukronatensenon ", and Lägerdorf, Holstein, Germany—Senonian, zone of *Gonioteuthis* [*Actinocamax*] *quadrata.*

**L. horsleyensis* Lang. A poorly preserved specimen has been recorded by Didon (1958 : 80, 84, text-fig. 2) from the Santonian of Le Trait, near Rouen, Seine Inférieure, France.

L. lagena Lang. Also recorded by Voigt (1930 : 495, 542, 560, pl. 26, fig. 9). Balsburg. " Mammillatensenon."

?*L.* [? = *Canupora*] *prima* (Kühn) (1930 : 65, pl. 26, fig. 13). Lithothamnienkalk. Haidhof, Ernstbrunn, Austria. Danian.

LEPTOCHEILOPORA

**Leptocheilopora filliozati* (Brydone). Also recorded by Gillard (1943 : 187). "... à la côte—72 m. par le forage Font-de-Chèvres ... Royan ", France. Either Senonian, zone of *Belemnitella mucronata*, or Maastrichtian.

**L. magna* Lang. Holotype and paratype—Lüneberg, Hanover, Germany—very probably boreal Maastrichtian [as Senonian, zone of *Belemnitella mucronata*]. Other specimens—Hemmoor, Hanover, Germany—Maastrichtian, either zone of *Belemnella lanceolata* mut. *sumensis* or zone of *B. junior*. Also recorded by Voigt (1930 : 496, pl. 27, fig. 5) ? Maastricht. Maastrichtian [as " Obere Mukronatenkreide "], and from Rügen, probably boreal Maastrichtian. The species is synonymous with *Barroisina galeata* Levinsen (1925 : 385, pl. 6, fig.

67). Møen, Aalborg, Denmark. Lower Maastrichtian [as Skrivekridt, Senonian, zone of *Belemnitella mucronata*]. The species is probably synonymous also with *Leptocheilopora longuesensis* Lang (1916*a* : 396, 397 ; 1921 : 76)—horizon recorded as " Campanian, Longuesse, France ".

PELMATOPORA

**Pelmatopora brydoneis* [*sic*] Lang. Recorded by Didon (1958 : 83, 85, text-fig. 10) from the Santonian of Elbeuf, near Rouen, Seine Inférieure, France.

**P. chrysalis* (d'Orbigny). Photograph only. Villedieu, France. Senonian, Coniacian. Also recorded by Gillard (1942 : 90) from the Upper Chalk between 24 m. 50 and 26 m. 80 (Division D) from a boring at Montbazon, south of Tours, Indre-et-Loire, France.

P. ? daniensis Voigt (1925*b* : 99, 100, pl. 3, figs. 4–6 ; 1930 : 514, 561, pl. 31, fig. 11). Cöthen. Danian.

**P. fecampensis* Lang. Holotype and other specimens—Fécamp north-east of Le Havre, Seine Inférieure, France. Senonian, Coniacian. Also recorded by Didon (1958 : 82, 84, text-fig. 9) from the Santonian of Le Trait, Elbeuf and Orival, near Rouen, Seine Inférieure, France.

**P. fragilis* (d'Orbigny). Lectotype—the specimen figured by d'Orbigny (1851, pl. 717, fig. 9). Fécamp, north-east of Le Havre, Seine Inférieure, France. Senonian, Coniacian. Photograph only of a specimen from the same locality and horizon as the lectotype, and a specimen from St. Avertin, south-east of Tours, Indre-et-Loire, France. Senonian, Coniacian. Also recorded by Gillard (1942 : 90) from the Upper Chalk between 6 m. 50 and 7 m. 30 (Division A) from a boring at Montbazon, south of Tours, Indre-et-Loire, France.

**P. larva* Lang. Holotype and D.28438—La Ribochère, Loir-et-Cher, east of La Chartre-sur-le-Loire, Sarthe, France. Senonian, Coniacian.

**Pelmatopora* cf. *marsupitum* [*sic*] Lang. Recorded by Didon (1958 : 83, 85, text-fig. 11) from the Santonian of Moulineaux, near Rouen, Seine Inférieure, France.

**P. d'orbignyi* Lang. Holotype. St. Avertin, south-east of Tours, Indre-et-Loire, France. Senonian, Coniacian. Specimen also from La Ribochère, Loir-et-Cher, east of La Chartre-sur-le-Loir, Sarthe, France. Senonian, Coniacian.

**P. quadrata* Lang. Synonymous with *P. filliozati* Lang. Photograph only of the holotype of *P. filliozati* Lang, from Fécamp, north-east of Le Havre, Seine Inférieure, France. Senonian. Coniacian.

**P. striata* (d'Orbigny). Lectotype—the specimen figured by d'Orbigny (1851, pl. 686, fig. 10). Nehou, south of Valoignes, east of Sainte Colombe, Manche, France. Senonian. Photographs only of a specimen from Villedieu, France. Senonian, Coniacian. Also recorded by Gillard (1942 : 90) from the Upper Chalk between 24 m. 50 and 26 m. 80 (Division D) from a boring at Montbazon, south of Tours, Indre-et-Loire, France.

**P. suffulta* (Brydone). Canu (1911 : 252, pl. 6, figs. 7–10) has also recorded " *Cribrilina insignis* " which is possibly synonymous with *Pelmatopora suffulta*. Roca, Argentine. Rocanean.

UBAGHSIA

Ubaghsia aurita Lang. Photograph only of the holotype. Royan, south of Rochefort, Charente Inférieure, France. Maastrichtian.

**U.* [*Batrachopora*] *coaxans* (Lang). Rügen. Probably boreal Maastrichtian [as " Upper Senonian "].

**U.* [*Batrachopora*] *crassa* (Lang). Rügen. Probably boreal Maastrichtian [as Senonian, zone of *Belemnitella mucronata*].

U. [*Steginopora*] *demorgani* (Jullien) (Jullien, 1886 : 615, pl. 19, figs. 4, 5, pl. 20, fig. 1). Les Molineaux, Meudon, south-west of Paris, France. Senonian, zone of *Belemnitella mucronata.*

U. [*Steginopora*] *meudonensis* (Jullien) (Jullien, 1886 : 614, pl. 17, figs. 1–5, pl. 18, figs. 1–3). Details as for *U. demorgani.*

U. [*Steginopora*] *ocellata* (Jullien) (Jullien, 1886 : 614, pl. 19, figs. 1–3). Port Brehay, north-east of Gourbesville, north-west of Carenten, Manche, France. " Etage sénonien "—probably middle or lower part of zone of *Belemnitella mucronata.*

**U. ornata* (Goldfuss). Lectotype—the specimen figured by Goldfuss (1826, pl. 9, fig. 1*b*). St. Petersburg, Maastricht. Maastrichtian. Specimens from Valkenburg (Fauquemont) and Maastricht, Holland. Maastrichtian. Also recorded by Voigt (1930 : 513, pl. 31, fig. 20 only). Maastricht. Maastrichtian [as " Ob. Mukronatensenon "].

U. [*Batrachopora*] *perforata* (Marsson) (Marsson, 1887 : 98, 109, pl. 10, fig. 11). Rügen. Probably boreal Maastrichtian [as " Schreibkreide "]. Also synonymous with *Cribrilina brachiata* Levinsen (1925 : 377, pl. 8, fig. 24). Møen, Aalbourg, Denmark. Lower Maastrichtian [as Senonian, zone of *Belemnitella mucronata*].

**U.* [*Batrachopora*] *ranunculus* (Lang). Rügen. Probably boreal Maastrichtian [as Senonian, zone of *Belemnitella mucronata*]. Also recorded by Voigt (1930 : 515, 561, pl. 31, fig. 17) from the same locality and horizon.

**U. reticulata* (Ubaghs). Lectotype—the specimen figured by Ubaghs (1865, pl. 2*a*, fig. 7*c*). Valkenburg (Fauquemont) or Geulem, Maastricht, Holland. Maastrichtian, " Ober Bryozoenschichte " (horizon *f* of Ubaghs). Specimens from Maastricht, Holland. Maastrichtian. Also recorded by Voigt (1930 : 515, pl. 31, figs. 18, 39 only). Maastricht, Holland. Maastrichtian [as " Ob. Mukronatensenon "].

The age of some Upper Cretaceous horizons abroad, e.g. that of the Rügen Chalk, has more recently been proved different from that originally stated by some authors. In the above list such revision of horizons is indicated by giving the old opinion enclosed in square brackets.

Among the stratigraphical terms used in the above list " Coniacian " refers to beds equivalent in age to the zone of *Micraster cortestudinarium,* and " Santonian " to beds equivalent in age to the zones of *M. cor-anguinum* and *Marsupites testudinaris.* The following terms are revised or generally in use by foreign authors.

Granulatensenon. Chalk with *Gonioteuthis granulata* in Germany, approximately equivalent to the zone of *Marsupites testudinarius* in England.

Lithothamnienkalk of Haidhof. Part of the Austrian Upper Cretaceous series of Danian age.

Maastrichtian. The general use of this term as applied to English and foreign horizons has been discussed (p. 12).

Mammillatensenon. Part of the Trümmerkreide of Sweden, equivalent to the upper part of the zone of *Gonioteuthis* [*Actinocamax*] *quadrata* in Germany and England. Possibly also equivalent to part of the zone of *Belemnitella mucronata* in England (see Withers, 1935 : 71).

Møen Chalk, Aalborg, Denmark. Referred by Levinsen (1925) and others to the Senonian, zone of *Belemnitella mucronata,* but now known to be Lower Maastrichtian.

Oberes Mukronatensenon of Maastricht. Used by Voigt (1930) for the Cretaceous of the type locality of the Maastrichtian, termed subsequently by Voigt, and generally, Maastrichtian *s. str.*

Rocanean. Part of the Argentine marine Upper Cretaceous. Feruglio (1949 : 218) gave an extensive survey of previous studies of the Rocanean and concluded that " after various considerations and a critical study of the data hitherto published by previous authors it is impossible, in the present state of knowledge, to decide whether these strata belong to the Upper Cretaceous or to the lower part of the Tertiary " [translation].

Rügen Chalk. Originally (e.g. Lang, 1921 ; 1922) regarded as Senonian, zone of *Belemnitella mucronata*, but subsequently shown (e.g. Voigt, 1951 ; Hiltermann, 1952) to be probably boreal Maastrichtian.

III. NOTES ON THE COLLECTIONS STUDIED

British Museum (Natural History)

Most of the material described here is from the large collections of Chalk Polyzoa made by C. T. A. Gaster and presented by him in recent years. The total of Chalk Polyzoa in the Gaster Collections numbers many thousands, the majority of specimens coming from south-east England. Much of the material has been carefully cleaned, stained and mounted by the collector, and all specimens are accompanied by full and precise details of locality and horizon.

A number of specimens have been studied which were obtained by earlier collectors. Such specimens, from collections other than the Gaster Collection, were incorporated by Lang in his works on Cretaceous cribrimorph Polyzoa and have been re-examined here to complete the revision of some genera.

The British Museum Collections also include photographs of specimens in the F. Canu Collection, Paris.

Sedgwick Museum, Cambridge

The R. M. Brydone Collection of Chalk Polyzoa in the Sedgwick Museum, Cambridge, includes many very well preserved cribrimorph Polyzoa. I have examined the type specimens of the species established by Brydone which belong to the genera revised here.

Norwich Castle Museum

All available specimens of cribrimorph Polyzoa in the R. M. Brydone Collection of Chalk fossils from Norfolk and adjacent areas have been examined. Where appropriate, these, and specimens from other collections in the Norwich Castle Museum, are incorporated in the present study.

IV. PRESERVATION OF THE MATERIAL

Cretaceous cribrimorph Polyzoa are often well preserved. They may, however, have been worn before interment so that projecting structures, such as avicularia, oral spines and median processes of the apertural bar, are eroded and rounded. Usually it is possible to find, in a zoarial fragment of average size, an area in which the zooecia are well preserved—often through being at a slightly lower level than the general surface of the zoarium and thus escaping the general effects of wear.

In contrast, some zoarial fragments entirely lack fine skeletal details, but retain, unbroken, projecting structures such as avicularia. General fine wear of this kind was possibly produced by solution effects on the surface of the skeleton before burial, rather than by mechanical abrasion. Phleger, Parker & Peirson (1953 : 117–119, pl. 12) have described and figured a number of Recent foraminifera with calcareous tests which exhibit similar primary solution effects. As only a few zoarial fragments of Cretaceous Polyzoa, from any given locality, may show such solution effects, it seems probable—as with the Recent foraminifera—that solution was predepositional rather than secondary.

The secondary cause of loss of detail in Chalk Polyzoa is recrystallization of the calcium-carbonate of their skeletons. This seems to have occurred more commonly in specimens from earlier horizons of the English Chalk.

Most polyzoan skeletons from the Chalk are composed of finely crystalline calcium-carbonate, but some may be perfectly replaced secondarily by silica. Siliceous specimens are usually very well preserved and may occur in the hollow centres of flint nodules forming part of the infilling " flint meal ".

V. TECHNIQUES

All the material has been examined with strong reflected light at high- and low-power magnifications under a binocular microscope. Lang's method of staining specimens with indigo water-colour has been used extensively (Lang, 1921 : lxxv). Without staining, the detailed characters, such as the type and number of pelmata, are hardly visible, but the careful application of a fairly dark, temporary stain brings out such details and differentiates the polyzoan skeleton from any adherent Chalk matrix.

Many specimens encrust fragments of echinoid test or pieces of *Inoceramus* shell. With such specimens, soaking in water and gentle brushing with a soft water-colour paint brush is usually an adequate cleaning method. Unattached zoarial fragments may be freed from their Chalk matrix by repeated soaking in water and gentle brushing.

The matrix may be harder and more closely adherent to the polyzoan skeletons. In these cases, soaking for a short time (10–30 minutes) in a saturated solution of salicylic acid was found to be sufficient to loosen the matrix without damaging the polyzoan. This treatment was always followed by careful washing in running water for 24–36 hours, the material being finally dried out very slowly. Specimens treated in this way have shown no signs of deterioration after five years. The material can be stained in the usual way.

Where possible, the specimens have been mounted with gum tragacanth on mahogany microscope slides—the system used generally in the Department of Palaeontology of the British Museum (Natural History).

Accurate drawings of specimens have been made on koda-trace mounted on squared paper using a micrometer scale and squared graticule in the eyepiece of the microscope. All holotypes and some other specimens have been photographed by reflected light generally at a magnification of ×20, but occasionally at higher magnifications up to ×100 to show minute detail.

VI. MORPHOLOGY OF CRETACEOUS CRIBRIMORPH POLYZOA

Zoarial Characters

GROWTH HABIT. Many Cretaceous cribrimorph Polyzoa have encrusting zoaria firmly attached to a substrate such as an echinoid test or the shells of other organisms. Unattached zoarial fragments are also common, but many of these may have been encrusting during life on some perishable object which was destroyed during or after fossilization. Thus the distinction often made between encrusting and so-called " free " forms is very uncertain. Bassler (1953 : G7) pointed out that " although often described as free, only the upper branches actually are free, for most bryozoans are attached basally or by other parts of their surface to extraneous objects . . .".

Encrusting zoaria are usually unilaminar, consisting of a relatively widespread, single layer of zooecia attached dorsally to a substrate. Much less commonly, successive layers of zooecia may be superimposed producing a multilaminar zoarium of hemispherical or nodular form : some species of *Polycephalopora* (Lang, 1922: 105) are of this type.

Unattached zoaria may be uni-, bi- or multilaminar, and, as fossils, are almost invariably fragmentary. Unilaminar fragments may originally have encrusted a destructible substrate since lost. Their dorsal surfaces may be fairly even, with the basal wall of each zooecium smooth, slightly convex, and separated from adjacent zooecia by a slight furrow ; or they may be more irregular, the basal wall of each zooecium possessing small, scattered tubercles, with deeper furrows between adjacent zooecia, as in *Pelmatopora gregoryi* (Brydone), *P. somptingensis* Lang (Pl. 15, fig. 4) and *P. brydonei* Lang (Text-fig. 77). Some Recent Polyzoa are attached to destructible substrates by means of tubercles protruding from their dorsal surfaces, and so their presence in fossil forms may indicate an originally adherent zoarium.

Some zoaria are bilaminar, consisting of two layers of aligned zooecia growing back to back, their dorsal surfaces united. Bilaminar zoaria may be irregularly lobed expansions in one plane, or more complex, foliaceous and undulating. From very small fragments of fossil bilaminar zoaria it is usually not possible to decide what was the original form of whole colonies, though they were presumably like Recent bilaminar polyzoan colonies. Some zoaria of *Pelmatopora larva* Lang (p. 134) are bilaminar.

Unattached fragments of multilaminar zoaria occur, but these may have been broken from encrusting masses.

Castanopora voigti sp. nov. (p. 236) has an erect, cylindro-quadrate zoarium in which four adjacent rows of zooecia alternate : this zoarial form is apparently rare among cribrimorph Polyzoa. Other erect, cylindrical zoaria occur occasionally, as in *Pnictopora suffocata* Lang and *P. strangulata* Lang.

Some genera, now largely archaic, were based on zoarial growth forms alone. There is often a considerable amount of variation in the growth habit of zoaria of the same genus or species. However, Lang (1916*a* ; 1921 ; 1922) frequently used zoarial growth habit to distinguish species which are otherwise morphologically identical. In the material revised and described here, *Pelmatopora* affords several examples of species established by Lang on zoarial growth form alone. Thus he distinguished (1922 : 300) as *P. roedeanensis*, a species differing " only in colonial habit from *P. marsupitum* [*sic*]." *P. lacuum* Lang was described (1922 : 324) as " *Pelmatopora ranunculoides*, but with an erect unilaminar asty [zoarium] ", and *P. promontoriorum* Lang (1922 : 320) as having a structure which " resembles that of *Pelmatopora saltdeanensis*, but the asty is erect instead of incrusting ". Again, Lang stated (1922 : 308) " *Pelmatopora damicornis* differs from *P. gregoryi* and *P. palmata* in its colonial habit, which is bilaminar. The three species thus form a progressive series with regard to colonial habit and condition, culminating in the erect bilaminar *P. damicornis* ".

Further examples may be cited, from genera not revised here. Among these are *Sandalopora lavardinensis* Lang distinguished (1922 : 330) on zoarial growth form from *S. gallica* Lang, *S. suppulosa* Lang separated (1922 : 331) on the same basis from *S. crepidata* Lang and three species of *Rhabdopora* (*R. virgata*, *R. virgulata* and *R. tigrina*) distinguished (Lang, 1916*a* : 405 ; 1921 : 209) in the same way.

Lang was aware of the uncertainty of describing unattached unilaminar zoarial fragments as " erect ". He stated (1919*d* : 196) " It is hard to be certain . . . that an apparently erect unilaminar asty is not really incrusting, since an alga or other perishable substance may have formed its support . . . it is unusual, however, to find an habitually-incrusting form in an apparently free condition, and, unless there are other reasons against it, I should advocate keeping incrusting and free, unilaminar forms specifically distinct ". Lang preceded this statement with the assertion that " in the Pelmatoporinae, and throughout the phylum, the direction of evolution is from an incrusting to an erect asty ".

In some Recent Polyzoa it is possible to find species, such as *Steganoporella buski* Harmer, in which different parts of the same zoarium are encrusting or erect and uni- or bilaminar and, in some parts, even multilaminar. On such evidence, and in view of the uncertainty of establishing whether or not an unattached, unilaminar zoarial fragment had an encrusting mode of life, I do not agree with Lang's division of species on zoarial growth habit alone. On the same evidence, the suggested " direction of evolution " from encrusting to erect zoaria must also be questioned.

ZOARIAL BUDDING. In an encrusting zoarium the zooecia may be developed uni- or multiserially. In Cretaceous cribrimorph Polyzoa the former condition is much rarer than the latter.

Uniserial encrusting zoaria. Some genera, such as *Corymbopora* and *Andriopora* (p. 266), are always uniserial, and the zooecia may possess caudae, as in *A. major* sp. nov. (p. 268). Generally, uniserial encrusting zoaria are more extensive than multiserial, though many more zooecia may be present in a multiserial zoarium which has developed uninterruptedly on a wide substrate. The angle of divergence of lines of uniserially budded zooecia may vary considerably.

Multiserial encrusting zoaria. These are usually fan-shaped, tending ultimately to become circular as more and more zooecia are developed. The sequence of growth appears to be like that observed by Marcus (1926) [summarized by Harmer, 1931 : 122] in the Recent cheilostome polyzoan *Electra pilosa* (Linn.). Here three distal buds arise from the ancestrula producing the first generation of zooecia. Successive generations are budded off producing a young fan-shaped colony, the distal-lateral edges of which are early reflected and usually meet on the proximal side of the ancestrula. Where zooecia are crowded, usually only one bud is produced, and in later stages there is a tendency to form adjacent, but distinct, uniserial, radiating rows of zooecia (e.g., as in *Aeolopora distincta* Lang, Pl. 2, figs. 1, 2). Where sufficient space is available two or three buds may arise in *Electra pilosa*, and a new radiating row of zooecia is intercalated in the colony. This feature is commonly found in Cretaceous cribrimorph Polyzoa.

In an adult zoarium, which has attained a more or less circular form, new zooecia are budded off from the periphery. This growing edge is seldom preserved in the Cretaceous cribrimorph Polyzoa ; presumably zooecia which have only just developed are more fragile than the preceding established, probably more calcified, adult zooecia.

As a multiserial zoarium matures, particularly if its substrate is limited, the later stages of zoarial growth may obscure the ancestrular area, often by the development of secondary calcareous tissue. Frequently one part of a zoarium may develop more rapidly than another, and, especially where there is a limited substrate, two zoarial expansions may converge, producing distortion of zooecia where they meet.

Bilaminar, erect, branching or foliaceous zoaria are apparently always multiserial. They may exhibit some of the features described for encrusting zoaria, but the modifications imposed by a limited substrate are usually absent, and the zoaria develop uninterruptedly.

Zooecial Characters

Certain structural features are common to the zooecia of all Cretaceous cribrimorph Polyzoa. They all possess calcified proximal, distal and lateral walls, and a secondary front wall (the frontal shield) composed of costae. These over-arch an aperture which is divided by an apertural bar from a distal orifice with marginal oral spines. This basic arrangement may be complicated in various ways—lateral costal fusions may develop between adjacent costae ; a median process, formed on the apertural bar, may fuse with the proximal pair of oral spines producing a proximal oral shield ; or the oral spines may be enlarged and bifurcated. The basic morphology is often further obscured by a general accumulation of secondary calcareous material which may fill the interzooecial valleys and, in some genera, encroach on to the frontal shields, or which may accumulate round the primary orifice producing a tubular secondary orifice. Ovicells and various heterozooecia may also obscure the form of zooecia.

The following observations and remarks apply to adult zooecia, but many of the characters discussed are the same in younger stages of zoarial growth. Young zooecia and ancestrulae are discussed later.

SIZE OF ZOOECIA. In the Cretaceous cribrimorph Polyzoa, as in other divisions of the Cheilostomata, the size of zooecia varies greatly, but some genera, compared with others, may have consistently small zooecia. For example, the zooecia of *Aeolopora* are always much smaller than those of *Castanopora*. However, for a given species there may be considerable differences in size between zooecia of separate zoaria, and often between zooecia in the same zoarium. Zooecial size, therefore, should seldom be used as a basis for differentiating species in the absence of more definite characters. But Lang has described (e.g. 1921 : 224–227) as separate species, forms such as *Dishelopora binoculata* and *D. claviceps*, which differ only very slightly in their zooecial length.

SHAPE OF ZOOECIA. It is strictly correct to say that in the great majority of cribrimorph Polyzoa the zooecia are polygonal and not broadly oval or elliptical. This polygonal form is most easily seen on the dorsal surfaces of unattached unilaminar zoaria (as in *Pelmatopora somptingensis* Lang, Pl. 15, fig. 4), or in encrusting zoaria in which the frontal shields have been destroyed, revealing the vertical walls of the zooecia. On the front of the zoarium interzooecial secondary tissue may obscure the true limits of each zooecium, or the frontal shields of adjacent zooecia may appear almost contiguous as in the specimens of *Castanopora* shown in Pl. 17. The upper surfaces of zooecia may vary in shape from almost circular to almost quadrate, though they are most commonly longitudinally oval.

In a given zoarium, most zooecia have approximately the same shape, but a few usually differ, possibly because of growth restrictions imposed by a limited substrate. Apparently, if only a limited amount of space is available for development, a zooecium tends to fill that space—its shape being to some extent controlled by it.

Zooecial Walls other than the Frontal Wall

Basal walls. A distinction may be made between the zooecia of some unilaminar encrusting zoaria and those which are now unattached. In the former, where the frontal shield is removed by wear, or artificially, there is often no indication of a calcified basal wall. This is shown in broken zooecia of *Lagynopora* and *Hexacantho-*

pora (Pl. 5, figs. 1, 4). In contrast, zooecia of unilaminar encrusting zoaria of *Pelmatopora* usually have a substantial calcified basal wall.

The zooecia of unattached uni- and bilaminar, or erect cylindrical zoaria always possess calcified basal walls, which may be smooth on their lower surface or have a number of scattered tubercles, as in *Pelmatopora somptingensis*.

Lateral, proximal and distal walls. These vary in height, and may slope as in *Lagynopora* and *Leptocheilopora*. Large distal and lateral communication pores may be visible in the distal and lateral walls respectively. These are often seen in *Lagynopora, Hexacanthopora* and *Leptocheilopora* and, less frequently, in other genera. The distal communication pores are usually large, single, circular or oval, and may be regarded as septula possibly covered originally by multiporous septular discs. Ordinary septula are usually smaller. The lateral communication pores are smaller than the distal, but more numerous. Often three or four occur in line along the middle of each lateral wall, or they may be scattered. Distal and lateral communication pores are visible in the specimen of *Leptocheilopora magna* shown in Pl. 6, fig. 5, and in the single zooecium of *Castanopora magnifica* shown in Text-fig. 112. In the latter their structure is unusual: small, circular pores occur in the centres of oval depressions surrounded by low rims. Communication pores have not been seen in *Pelmatopora* or other genera: septula are probably present but very minute. Dietellae occur in *Lagynopora, Hexacanthopora* and *Leptocheilopora*—they are visible, for example, in some zooecia of *Hexacanthopora sexspinosa* Lang (Pl. 5, fig. 3).

FRONTAL WALL. Lang (1921 : xxxvi) described the frontal wall of membranimorphs, from which the cribrimorphs are to be derived as a " composite structure. Laterally and proximally it is calcareous [the gymnocyst], and slopes outwards, gradually becoming continuous with the lateral walls; but all the middle and distal parts [the aperture] are occupied by a flat and chitinous roof ".

In the Cretaceous cribrimorph Polyzoa a secondary frontal wall of costae (the frontal shield) is formed over the aperture, the only part of the primary frontal wall to be retained being the calcareous gymnocyst surrounding the aperture. The frontal membrane, or chitinous part of the primary frontal wall originally covering the aperture, is not preserved.

PRIMARY FRONTAL WALL—GYMNOCYST. The gymnocyst is apparently always smooth. It is variable in width, usually wider proximally to the frontal shield and narrower along its sides. Occasionally a narrow band of gymnocyst may extend round the distal and lateral margins of the orifice. The amount of visible gymnocyst is commonly diminished by close growth of the zooecia, and, in many genera of Cretaceous cribrimorphs, it is totally concealed by plentiful interzooecial secondary tissue. As in some species of *Pelmatopora*, the secondary tissue may contain lacunae through which the gymnocyst is locally exposed.

SECONDARY FRONTAL WALL—FRONTAL SHIELD. The general and detailed features of the frontal shield, and its relationship to other zooecial characters, provide one of the most useful means of differentiating genera and species in the Cretaceous cribrimorph Polyzoa. Essentially, the frontal shield is composed of a series of costae which develop from the edge of the gymnocyst and overarch the aperture, usually fusing along the mid-line of the zooecium. This basic arrangement is complicated in various ways. There is often considerable morphological similarity between the frontal shields of fossil cribrimorphs and those of some of the Recent Cribrilinidae. The development of some features in Recent species (observed by Harmer and others) shows that some analogous characters in the fossils may have had an origin different from that suggested by Lang.

Development and structure of the costae. Hincks has described the costae of Recent Cribrilinidae, such as those of *Membraniporella nitida* (Johnston) as " probably the equivalent of the marginal spines on many of the Membraniporae ". Harmer (1902 : 292) agreed with Hincks's opinion and again mentioned *M. nitida*, suggesting that the modified, overarched, marginal spines developed by closure of embayments in the edge of the gymnocyst (Text-fig. 2*A–C*). Harmer also figured (1902, pl. 15, fig. 7) the ancestrula and some young zooecia of a specimen of *Cribrilina radiata* (Moll), in which he suggested the costae are analogous to horizontal calcareous lobes occurring on the inner sides of the marginal spines of the Membraniporid ancestrula. Norman (1903 : 91) described a more complex development of costae and has shown that lumen pores and lateral costal fusions may be formed as the costae develop. Costae of four of the species described by Norman are shown in Text-fig. 2*D–G*, p. 27.

Other modes of formation of costae were recorded, somewhat obscurely, by Waters (1923 : 545–573). Apparently, in the Recent species *Lepralia otto-mulleriana* (Moll), a thin calcareous lamina may gradually spread from the proximal and lateral margins of the aperture leaving uncalcified pores. Subsequently, irregular ridges may separate costa-like areas, each with one pore (Text-fig. 3*C*). In other specimens, irregular " broad spines " with small " nodulations " may spread secondarily from the proximal and lateral margins of the aperture and so produce a costate appearance (Text-fig. 3*A*, *B*, p. 28).

Thus the costae of different and the same species of Recent Cheilostomata may differ structurally and have developed in different ways. In those forms in which the costae are produced by apparent closure of embayments in the edge of the gymnocyst the costae are continuous tubular structures. The costae of all the Cretaceous cribrimorph Polyzoa described here appear to be of this type. It is possible that a costa with the structure described by Norman (1903) is not a simple tubular outgrowth of the type described by Harmer. Lumen lines may have been present in the costae of some Cretaceous species, but fine detail of this kind is easily destroyed during fossilization.

Harmer has pointed out that Lang's studies confirmed palaeontologically the supposed Membraniporid origin of Recent forms with costate frontal shields. Lang (1921 : 6, text-fig. 5) compared Membraniporid and cribrimorph Polyzoan structures —his text-figure is reproduced here, somewhat modified, in Text-fig. 4*A*, *B*, p. 29.

Number of costae. In the Recent Cribrilinidae and in the Cretaceous cribrimorph Polyzoa the number of costae in any single zooecium of a given zoarium may vary considerably. Illies (1953) even suggested that zooecial dimensions provide a better basis for specific diagnosis in species of *Rhiniopora* [*Castanopora*]. The number of costae is often greater in longer zooecia and fewer in shorter ones. Similarly, adult zooecia usually possess more costae than young zooecia in the same zoarium, though in some species the reverse may be true. Taken alone, the number of costae is thus of little diagnostic value, but, provided a sufficient number of specimens is available, the general range in number of the costae may be used, in conjunction with all other available characters, to differentiate species. Lang's statement (1919*d* : 197) that the number of costae " tends to increase during development [in the Pelmatoporinae] but may be very much reduced catagenically " indicates the variability of this character.

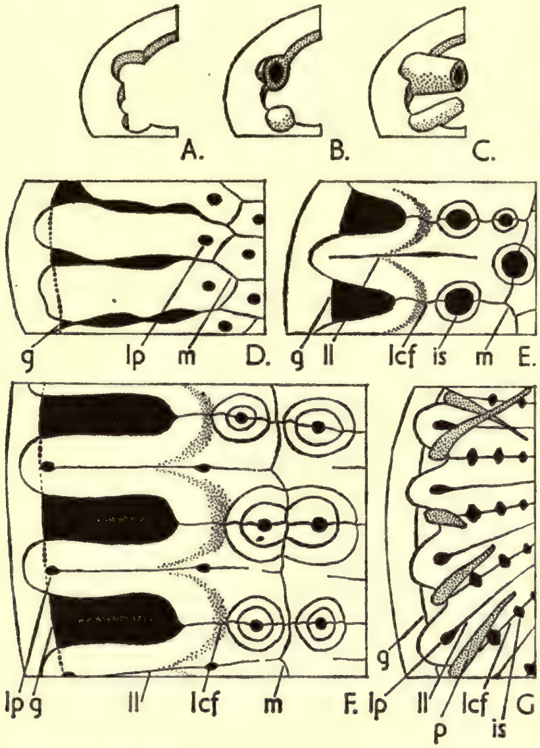

FIG. 2. *A–C*. Diagram showing the development of continuous tubular costae from closure of bays in the edge of the gymnocyst.

D " *Cribrilina annulata* Fabricus "—based on Norman's figure—1903, pl. 8, fig. 10.

E. " *Cribrilina balzaci* (Audouin) "—based on Norman's figure—1903, pl. 9, fig. 6.

F. " *Gephyrotes nitido-punctata* Smitt "—based on Norman's figure—1903, pl. 8, fig. 13.

G. " *Cribrilina innominata* Couch "—based on Norman's figure—1903, pl. 9, fig. 3.

g, edge of gymnocyst ; *is*, intercostal space or " lacuna " ; *l.c.f*, lateral costal fusion ; *ll*, lumen line ; *l.p*, lumen pores or pelmata ; *m*, median line of frontal shield ; *p*, non-calcareous papillae.

Lumen pores : pelmata : pelmatidia. The lumen pores which occur along the mid-line of each costa in some of the Recent Cribrilinidae are closely analogous to the pores which occur in the same position on the costae of many Cretaceous cribrimorph Polyzoa. However, Lang (1921 : xli) termed the latter *pelmata* and *pelmatidia*, and described them as " hollow upturned prolongations, presumably continued in the living organism as free spines, but appearing in the fossil as a row of broken ends ". In some species, such as the more complex forms of *Pelmatopora*, he distinguished " primary, secondary, tertiary and quaternary " pelmata and pelmatidia

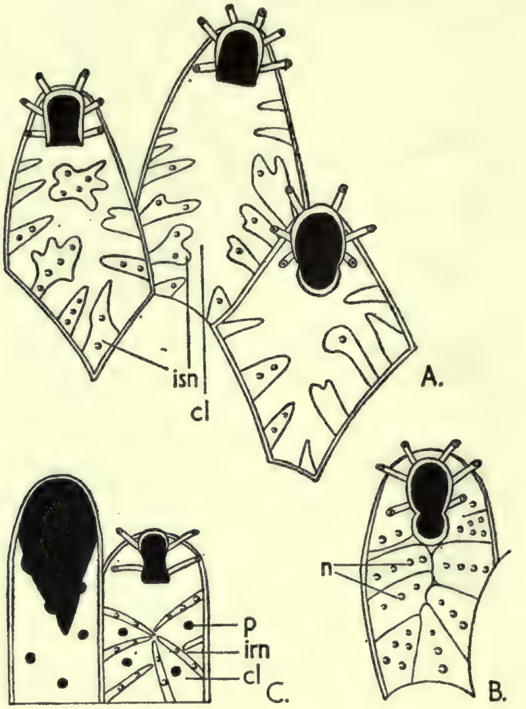

Fig. 3. Development of costa-like structures in the Recent species *Lepralia ottomulleriana* Moll. *A*, *B*, *C*, based on parts of Water's figures, 1923, pl. 17, figs. 1, 2 and 5 respectively.

c.l, thin calcareous lamina ; *irn*, irregular ridges with " nodulations " ; *isn*, irregular broad " spines " with " nodulations " ; *n*, " nodulations" ; *p*, pores.

corresponding in position to equivalent lateral costal fusions. The terms " primary, secondary " etc. were used with reference to the supposed order in which the pelmata developed and shifted outwards from the median area of the frontal shield. In agreement with Harmer (1926 : 471) I regard the pelmata and pelmatidia as lumen pores, which, as in the Recent Cribrilinidae, have developed during the formation of the costae bearing them. In Recent specimens, as a costa is formed, the lumen pores are apparently left as uncalcified, membranous areas on its upper surface. There is no indication that the pores are formed first at the inner end of the costa and subsequently migrate towards its outer end, an hypothesis with which Lang attempted to account for the position of pelmata and pelmatidia in most of the

Cretaceous forms. Thus Lang stated (1922 : 6) " It is convenient to consider that the primary [first formed] pelma has shifted proximally on the costa, carrying with it a part of the median line of fusion, and that the secondary pelma has been added at the distal [inner] end of the costa. . . . This process is repeated in more ad-

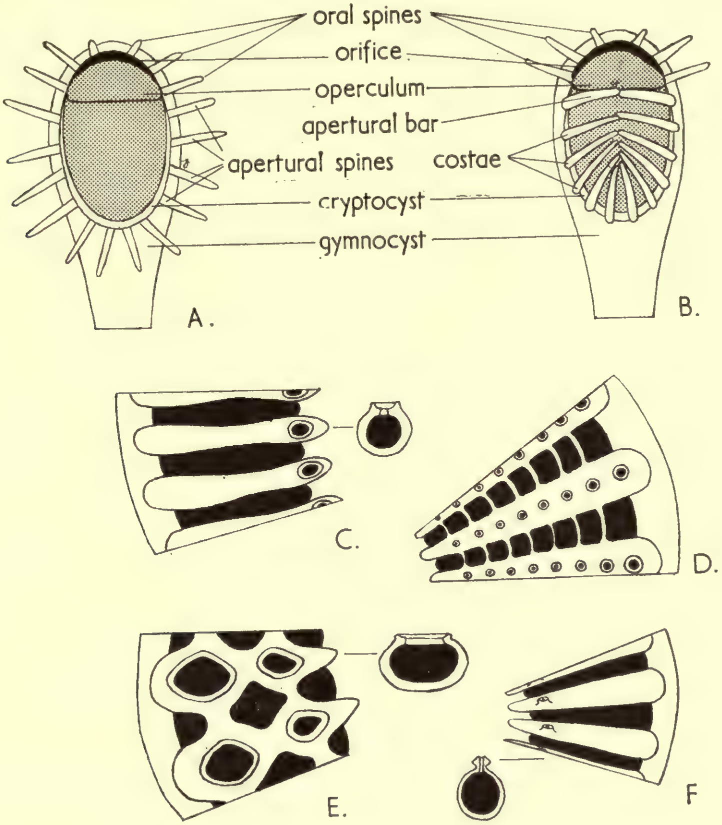

FIG. 4. *A*, *B*. Diagram showing the development of a cribrimorph polyzoan (*B*) from a Membraniporid (*A*). Modified from Lang (1921, text-fig. 5). Chitinous parts stippled.

C–F. Types of costae, pelmata, pelmatidia and lateral costal fusions in Cretaceous cribrimorph Polyzoa.

C. Simple Pelmatoporid costae with long, single intercostal spaces and each with a large, oval pelma at the inner end. The cross-section shows the slight rim round the pelmata.

D. Costae of *Castanopora* with numerous equally small pelmatidia and a corresponding number of lateral costal fusions, each curved parallel to the edge of the gymnocyst producing rows of somewhat oblong intercostal spaces.

E. Costae of *Ubaghsia* with two very large pelmata, short lateral costal fusions and irregular intercostal spaces. The cross-section shows that the costae are wider than in other genera.

F. Costae of *Aeolopora* each with a single boss-like pelmatidium and no lateral costal fusions. The cross-section shows the extended rim of the pelmatidia.

vanced species". He summarized the supposed process in a series of diagrams (1919*d* : 198, text-figs. 2–5 ; 1922 : 6, text-fig. 2).

Pelmata and pelmatidia, or lumen pores, were recorded by Lang (1916*a* : 83, 84 ; 1922 : 1) in all the genera which he assigned to the Pelmatoporidae. In the material studied here they have also been found in *Lagynopora*, *Hexacanthopora*, *Leptocheilopora* and *Aeolopora*. There is no reason to suppose, as Lang has done (1922 : 8), that the pelmata in *Diacanthopora* are the broken ends of branched spines. In agreement with Harmer (1926 : 471), I regard them also as lumen pores. Lang (1921) has recorded minute pores in the costae of *Pliophloea* (p. 172), *Dishelopora* (p. 217) and *Histricopora* (p. 227). Although he did not call these minute pores "pelmata" or lumen pores, I regard them as such. It is very probable that minute pelmata, discernible only under high-power magnification, are, or were originally, present in most of the Cretaceous cribrimorph Polyzoa but have been lost during fossilization.

Although Lang stated (1922 : 5), "It is not possible to impose a very rigid line of demarcation between a pelma and a pelmatidium", he has used the supposed difference between the two to separate some subfamilies. Very often, as in the more complex species of *Pelmatopora*, a graded series occurs with the largest lumen pore (pelma) at the outer end, successive pores becoming gradually smaller towards the inner end of each costa. In the simpler species of *Pelmatopora* and in *Tricephalopora*, there is often a single, large, oval pelma near the inner end of each costa. In *Castanopora* a series of up to seven or eight equally small pores may occur, or, as in *Aeolopora*, a single, minute, boss-like structure with a central pore may be present near the inner end of each costa. The pelmata may have a distinct rim produced by local thickening of the costal wall round the pore. This feature is also found in Recent forms ; Waters (1923) has recorded such thickened pore edges produced during the development of the secondary frontal wall in *Lepralia otto-mulleriana* (Text-fig. 3*C*). In other genera of Cretaceous cribrimorph Polyzoa lumen pores may not occur in a continuous series and may lack distinct rims, as in *Leptocheilopora magna* Lang (Pl. 6, fig. 1). The different types of pelmata and pelmatidia which occur in the Cretaceous material described here are shown in Text-fig. 4*C–F*.

Lang's terms "pelmata" and "pelmatidia" are retained in the systematic descriptions, but only for convenience of reference to the size of the pores : pelmata are interpreted as large lumen pores, and pelmatidia as small lumen pores. I do not accept in any way Lang's hypothesis of their origin.

Lateral costal fusions. Lang's concept of a "proximal shift" of pelmata and lateral costal fusions presupposes that both features are secondary modifications of the costae. In some Recent forms, however, lateral costal fusions, like the pelmata or lumen pores, are developed during the primary growth of the costae (Text-fig. 2*D–G*) ; in others they may develop subsequently between established costae and divide an originally long, single intercostal slit into a series of small intercostal spaces. It is difficult to decide whether the lateral costal fusions which occur in some Cretaceous cribrimorph Polyzoa are formed, like the pelmata, during the initial growth of the costae or subsequently. Pairs of lateral costal fusions usually coincide with the pelmata on the costae. Norman (1903) suggested that in some

Recent forms adjacent costae produce lateral processes which meet half-way between the two costae and fuse (Text-fig. 2*E*). In other cases he suggested that adjacent, irregular costae may touch at various points along their length producing apparent lateral fusions, e.g., in *Membraniporella nitida* (Text-fig. 2*D*). In the Cretaceous material most of the costae are regular and the lateral fusions between them are distinct tubular structures, often curved parallel with the edge of the gymnocyst (Text-fig. 4*D*). In some species, such as *Ubaghsia ornata*, in which the pelmata may be very large, the costae expand at the levels of the pelmata and the lateral fusions are correspondingly short (Text-fig. 4*E*). Lateral costal fusions are not always present where pelmata are developed—*Lagynopora*, *Hexacanthopora* and *Leptocheilopora* have pelmata but no lateral costal fusions. Although the number of lateral costal fusions on each costa of the same frontal shield is usually constant, the larger costae may possess extra fusions.

Intercostal spaces. As in the Recent Cribrilinidae, the intercostal spaces of Cretaceous cribrimorph Polyzoa vary widely in shape and size. In many genera the spaces between adjacent costae are elongate, single openings (Text-fig. 4*C*). In others a series of lateral costal fusions subdivides the space between adjacent costae into a number of smaller intercostal spaces termed, by workers on Recent forms, " lacunae ". The term " lacunae " is used here, however, to describe openings in the interzooecial tissue. In some species with lateral costal fusions the outermost intercostal spaces may be fairly constant in shape, but little diagnostic value can be placed upon this feature. In general, the intercostal spaces of the earliest, simpler, Cretaceous cribrimorph Polyzoa are wider than the costae they separate, but in the majority of later forms the reverse is true. The intercostal spaces may be filled with secondary calcareous tissue which spreads outwards from the median area of the frontal shield : this is well shown by some species of *Lagynopora*.

Median area of fusion. The size and shape of this area may vary considerably in a given species between zooecia of different zoaria and even between zooecia of the same zoarium. Many median areas of fusion are very narrow, involving only the inner tips of the costae and almost confined to the mid-line of the frontal shield ; others are wider and fusiform producing a flattened top to the arched frontal shield. In some species of *Lagynopora* and of other genera, the costae may be firmly united for about two-thirds of their length by an outward extension of the median area of fusion.

Lang's concept of a proximal shift along the costae of the pelmata and lateral costal fusions led him, in his descriptions of some Pelmatoporid species, to use the term " median area of fusion " to include all the frontal shield inside the outermost lateral costal fusions, which he regarded as parts of the original median area of fusion. Thus he described (1922 : 301) *Pelmatopora somptingensis* as having " two paired rows of perforations [intercostal spaces] in the original median area of fusion (now comprising the greater part of the intraterminal front-wall [frontal shield]) ". The median area of fusion of *P. somptingensis* is, in fact, very narrow (Text-fig. 96). The same remarks apply to other species with lateral costal fusions : these structures are not part of the median area of fusion. Different types of median areas of fusion, as defined here, are shown in Text-fig. 5*a–d*.

Apertural bars. Lang (1921 : 20) has shown that the apertural bar of the less complex, earlier genera of Cretaceous cribrimorph Polyzoa is asymmetrical but that in later more complex forms it is symmetrical and composed of two costae firmly fused in the mid-line. There is often considerable variation in its form between different genera and species, and occasionally between specimens of the same species. The apertural bar may be straight and relatively featureless, as in *Andriopora minor* sp. nov., or distinctly " V " shaped, as in *Leptocheilopora filliozati*. In *Hexacanthopora* *sexspinosa* it is curved with a prominent median process. In *Lagynopora* the median process of the apertural bar is more pronounced and usually bifurcated, producing two hollow spine-like processes which curve outwards from the mid-line of the orifice and fuse with the proximal-lateral oral spines forming a " Y "-shaped proximal oral shield.

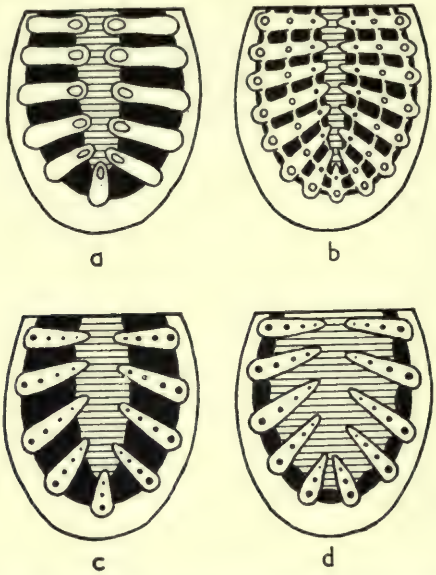

Fig. 5. Types of median area of fusion in Cretaceous cribrimorph Polyzoa.
a, Narrow median area of fusion found in less complex species of *Pelmatopora*; *b*, narrow median area of fusion typical of frontal shields with numerous lateral costal fusions—found in the more complex species of *Pelmatopora*; *c*, *d*, Langynoporid frontal shields, (*c*) narrow median area of fusion, (*d*) very wide median area of fusion. Median area of fusion shaded with horizontal lines.

The costae composing the apertural bar may also possess pelmata or pelmatidia if these are present in the costae of the frontal shield. Secondary calcareous tissue may accumulate on the apertural bar, as in some genera of the Tricephaloporinae, spreading proximally as a tongue of tissue covering the median area of the frontal shield. The whole apertural bar is easily modified by wear, median processes being particularly easily destroyed. Diagrams of different types of apertural bars developed in the material studied here are shown in Text-fig. 6*a*–*q*.

TERTIARY FRONTAL WALL. Continued upgrowth of interzooecial secondary tissue (p. 40), combined with lengthening and expansion of the tissue of tubular secondary orifices (p. 35), and parts of other secondary structures, produces a prominent, irregular tertiary frontal wall above the general level of the frontal shields. This composite type of tertiary frontal wall is well developed in some species of *Ubaghsia* (Pls. 21–23).

A less complex tertiary frontal wall is developed in some species of *Tricephalopora*. In some a tongue of secondary tissue, spreading from the apertural bar, forms part

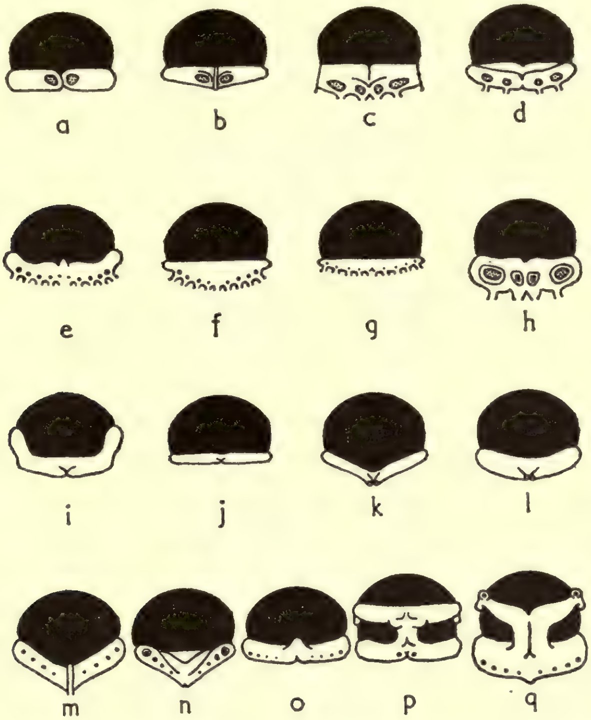

FIG. 6. Types of apertural bars found in Cretaceous cribrimorph Polyzoa.

a–d, Apertural bars of *Pelmatopora*. (*a*) *P. solearis*, (*b*) *P. d'orbignyi*, (*c*) *P. somptingensis*, (*d*) *P. palmata*. *e–g*, Apertural bars of *Castanopora*. (*e*) *C. magnifica*, (f) *C. castanea*, (*g*) *C. jurassica*. *h*, Apertural bar of *Ubaghsia ornata* with four large pelmata. *i*, *j*, Apertural bars of (*i*) *Andriopora major*, (*j*) *A. minor*. *k*, *l*, Apertural bars of (*k*) *Aeolopora distincta*, (*l*) *A. nebulosa*. *m*, *n*, Apertural bars of (*m*) *Leptocheilopora filliozati* showing the median ridge which is continued along the mid-line of the frontal shield and (*n*) *L. vulnerata* in which there is a prominent median facet on the distal side of the "V"-shaped apertural bar. *o*, Apertural bar of *Hexacanthopora sexspinosa* with prominent median process. *p*, *q*, Apertural bars of two species of *Langynopora* showing the bifurcated median processes and their fusion with the proximal-lateral oral spines, (*p*) *L. pustulosa*, (*q*) *L. ampulla*. For convenient comparison each orifice and apertural bar is drawn at approximately the same scale, irrespective of actual size.

of a tertiary frontal wall, in others this structure is combined with a general upgrowth of tubular secondary orifices and interzooecial secondary tissue to form a more complete tertiary frontal wall, which is less raised above the general level of the frontal shields than in *Ubaghsia.* Lang (1921 : xlix) has observed that " *Hippiopora* appears to be the only described Cretaceous Cribrimorph outside the Pelmatoporidae which possesses a tertiary front-wall ".

ORIFICES. The primary orifices of young zooecia vary in shape but are sharply defined, and, apart from being larger, may remain still sharply defined and otherwise unmodified in adult zooecia. Accumulation of secondary calcareous tissue round a primary orifice, or other modications, produces a secondary orifice.

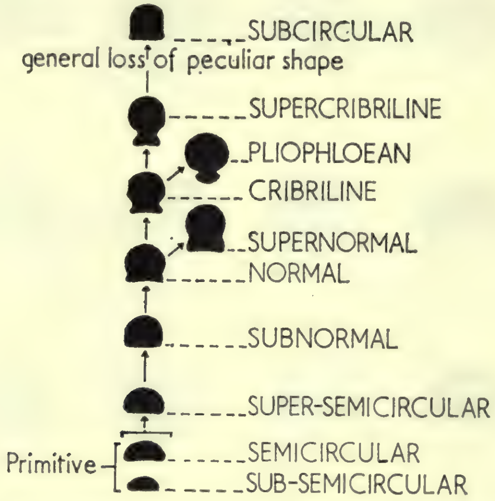

FIG. 7. Evolution and terminology of orifices suggested by Lang.
Diagram based on Lang (1921, text-fig. 10).

PRIMARY ORIFICES. Lang (1921 : xlvi) suggested that the primary orifice in Cretaceous cribrimorph Polyzoa, although varying in shape, tended to pass from a " primitive " so-called " sub-semicircular " or " semicircular " form to more complex shapes. This evolutionary sequence is summarized in Text-fig. 7 ; the terms used are those devised by Lang to describe ten different shapes which he recognized. He was well aware of the uncertainty of suggesting such a sequence, for he stated, " This evolution must not, however, be strained. It is easy to see how a normal aperture [orifice] may become distinctly pliophloean without passing through a cribriline stage ".

The present work shows how, in most genera, and often within a given species, the shape of the orifice can be very variable. This feature is discussed and illustrated in some detail under the remarks on *Leptocheilopora filliozati* (p. 115), of which many specimens are available. Similar remarks apply to other species of *Leptocheilopora* and to species of other genera. *Pelmatopora* often has a comparable range of variation in shape of the primary orifice. Where proximal-lateral constrictions occur in an orifice they may be more or less pronounced, and the shape of the proximal margin may vary according to the form of the apertural bar. Conversely, but in only a few species, the orifice may have a fairly constant shape, as in *Leptocheilopora magna* Lang.

Thus the shape of the primary orifice is not usually of diagnostic value. It may vary in shape naturally or its form may be changed by wear ; probably the median proximal notch found in some orifices of *Leptocheilopora tenuilabrosa* (p. 107) is due to wear. No general evolutionary sequence in the shape of the primary orifice could be distinguished in the material studied here.

In contrast to the variable shapes which may occur, the length and breadth of the orifice in a given species are often constant within a very small range. Lang (1919*d* : 198) only briefly considered the size of the orifice in relation to that of the frontal shield, and suggested " This tends, as a rule, to increase ; but, in some cases . . . becomes smaller catagenetically ". In the genera studied here it is difficult to find evidence to support this view. It is apparent, however, that in a given species the length (*hr*) and the width (*lr*) remain fairly constant although the shape may vary. This feature is again well shown by *Leptocheilopora filliozati* (p. 115) in which the dimensions of the orifice, irrespective of its shape, are fairly constant, even in abnormal zooecia.

Lang has suggested (1919*d* : 197) that the shape of the orifice " tends to alter from being rather longer than wide to rather wider than long ", or, in other words, that *lr* generally exceeds *hr* in later genera and species. In those genera revised here in which the form of the primary orifice is not secondarily modified in the adult stages, I can find no indication of this tendency. It is apparent that species with orifices which are wider than high predominate throughout.

SECONDARY ORIFICES. In many genera the primary orifice is modified in adult zooecia by the marginal accretion of secondary calcareous tissue. A slightly thickened oral rim may be developed as in *Pelmatopora*, or increased accumulation may produce a tubular secondary orifice, as in some species of *Tricephalopora*. Other structures, such as oral spines and avicularia, may be incorporated in the general upgrowth of calcium-carbonate round the orifice, as in *Ubaghsia*, or distinct distal and proximal oral shields may be produced, as in *Lagynopora*.

Where a slightly thickened oral rim is developed the secondary tissue is usually accumulated fairly evenly round the distal and lateral margins. The proximal margin of the orifice, formed by the apertural bar, is seldom affected. Thus, although the dimensions of the orifice are slightly decreased they usually remain the same in proportion to one another and may be used, in conjunction with all other available characters, in specific diagnosis.

In genera with a tubular upgrowth of calcareous tissue round the primary orifice the secondary orifice is often very different in shape and size, and is separated from the primary orifice by a peristome of variable length. The formation of distal and proximal oral shields, incorporating other structures, is considered later.

ORAL SPINES. In some Recent cheilostome Polyzoa the shape and size of the oral spines varies widely even in a single species. Most oral spines are hollow in the centre, but they may be long, unbranched and rod-like, or bifurcated, or variously branched.

Frequently only the proximal-lateral pair of oral spines is branched, the remainder being unmodified. The oral spines are branched, for example, in some species of *Chaperia*, *Scrupocellaria* and *Amphiblestrum* (Text-fig. 9). The spines may be jointed near the base so that the upper part is easily removed by wear, leaving a small, hollow spine-base (Text-figs. 8*c*; 9*k–n*).

In most fossil specimens, including many of the Cretaceous cribrimorphs, only the bases of the oral spines are preserved. They may have been jointed near the base and have broken off at this point, or, as is more probable, they may have been unjointed and worn down to the base. Thus the apparent simplicity and similarity of the oral spines in many genera of Cretaceous cribrimorphs may be largely due to wear.

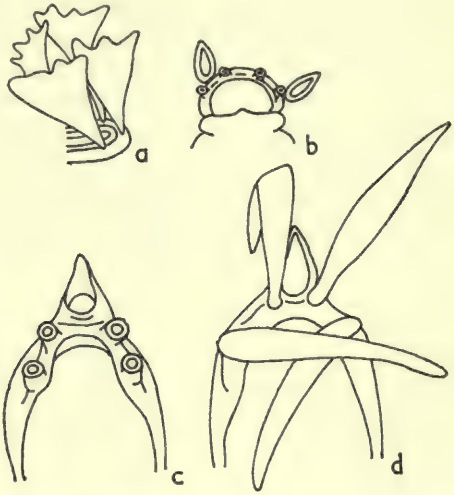

Fig. 8. Oral spines in Recent species.

a, b, Cribrilina alcicornis Jullien (1883, pl. 14, figs. 24, 25), (*a*) expanded, lobed oral spines preserved, (*b*) a worn orifice, the oral spines reduced to hollow spine-bases, and two worn avicularia. *c, d, Chaperia "quadrispinosa"* [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 549*c*], (*c*) distal end of worn zooecium with four hollow oral spine-bases and distal-median avicularium, (*d*) distal end of unworn zooecium with four complete oral spines and distal-median avicularium.

However, bifurcated and branched oral spines are preserved in some genera: *Ubaghsia* may possess branched spines, and some species of *Pelmatopora* have distinctive bifurcated oral spines. Jullien (1886, pls. 17–19) figured branched spines in *Ubaghsia* [*Steginopora*] *meudonensis*, *U.* [*S.*] *ocellata*, *U.* [*S.*] *demorgani* and in *U. reticulata* (see Pl. 22). All these species possess a substantial tertiary frontal wall which evidently protected the oral spines from wear. The variously modified oral spines which occur in some species of *Pelmatopora* were interpreted by Lang (1916*a*: 102; 1919*d*: 200; 1921: xxxiii–xxxiv; 1922: 247) as secondary avicularia which have replaced the oral spines. I have examined a very large number of specimens of *Pelmatopora*, including those seen by Lang, and have found nothing to suggest

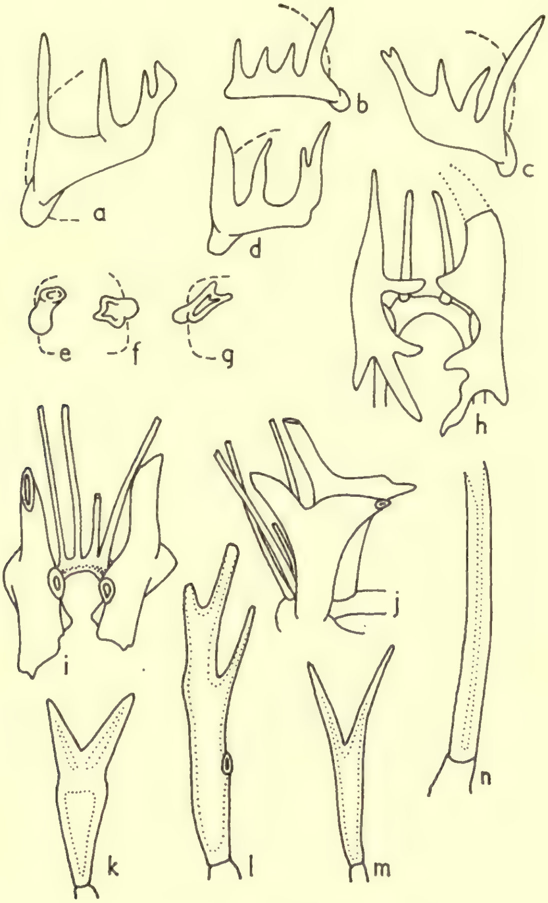

FIG. 9. Types of oral spines in three genera of Recent cheilostomatous Polyzoa.
a–d, "*Scrupocellaria frondis*" [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 31.12.19.7B]. Branched oral spines from four zooecia of the same zoarium. *e–g*, "*Scrupocellaria securifera*" [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 28.3.6.170]. Small oral spines tending to bifurcate. *h*, "*Amphiblestrum cervicorne*" [B.M. (N.H.) Zool Dept. Polyzoa Coll. slide 87.12.9.328]. Front view of paired, branched lateral oral spines and two unbranched distal oral spines. *i–j*, "*Chaperia* sp." [B.M. (N.H.) Zool Dept. Polyzoa Coll. slide TN 863A]. Front and side views of paired, bifurcated lateral oral spines and four unbranched distal oral spines. *k–m*, "*Chaperia cervicornis*". (*k*) [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 99.5.1.548]—stout, bifurcated oral spine, jointed at the base and with the central hollow visible; (*l*) [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 444D]—branched oral spine, jointed at the base and with large central hollow; (*m*) [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 99.7.1.1202]—bifurcated oral spine, jointed at the base. *n*, "*Chaperia galeata*" [B.M. (N.H.) Zool. Dept. Polyzoa Coll. slide 53B]. Unbranched oral spine, jointed at the base and with central hollow.

that the structures are avicularian. Their bifurcated form, as in *Pelmatopora gregoryi*, is a condition which is unknown in avicularia, and they lack true avicularian characters. They occur consistently as part of the symmetrically arranged series of spines round the orifice, and they are most closely comparable with the expanded and bifurcated oral spines which occur in some Recent cheilostome Polyzoa.

Lang (1916*a* ; 1919) has referred to the structures as " avicularia " and later (1921) as a " kind of (supposed) aviculoecia [avicularia] ". In his fullest description of *Pelmatopora* (1922) he was evidently undecided as to their nature. In a discussion of " the elaboration of the aperture [orifice] " he has stated (p. 244) " . . . what appears to be a new structure [in *Pelmatopora*] occurred on the distal edge of the secondary apertural [oral] rim, corresponding in position to the obliterated distal pair of apertural [oral] spines, though probably lying just outside them ; it is even possible that the apparently new structure was a new development of the apertural [oral] spines, as the evidence of specimen D.23397 of *P. brydonei* is not altogether conclusive. . . . In this specimen the right distal apertural [oral] spine and the new structure on the same side are both present and seem to be separate. On the other hand, the astogenetic evidence of *Pelmatopora saltdeanensis* [= *P. gregoryi*] points to this supposed new structure being but a development of the distal pair of apertural [oral] spines. . . . It is probable that, if not developments of apertural [oral] spines, these projections are aviculoecia [avicularia], and that the pointed depressions on their distal surfaces are the rostra. During evolution they enlarge, lengthen, and become bifid . . . ". In his section on the systematics of *Pelmatopora* Lang referred to the structures as " secondary aviculoecia ".

The structure in D.23397 is discussed in detail under the remarks on *P. brydonei* (p. 166) and is figured (Text-fig. 78*a*, *b*). It is an enlargement of the unmodified oral spine, and regeneration of the whole orifice (see Lang, 1922 : 294) has not occurred. As Lang suggested in his reference to the "astogenetic evidence" of *P. saltdeanensis* [= *P. gregoryi*] and in his remarks on that species (1922 : 319), a comparison of oral spines of young and adult zooecia in a given zoarium points to his " secondary aviculoecia" as only a development of the unmodified distal oral spines. In the species of *Pelmatopora* in which the adult zooecia possess enlarged oral spines,[1] the young zooecia have unmodified spines which gradually become expanded or bifurcated as the zooecia mature.

In a given species of *Pelmatopora*, as in Recent cheilostome Polyzoa, the size and shape of the enlarged oral spines may vary considerably. This variation, which is produced largely by different degrees of wear, is shown particularly in Text-fig. 81*a–d* (*P. marsupitorum*), Text-fig. 88*a–f* (*P. gregoryi*), Text-fig. 97*a–g* (*P. somptingensis*), and in Text-fig. 101*a*, *b* (*P. palmata*). It follows that variations in shape of the enlarged oral spines are not always suitable characters on which to differentiate species.

The oral spines are always arranged symmetrically around the orifice, whatever their number. They are often equally spaced, but occasionally occur in paired groups of two or three. In the material studied, the adult zooecia in some genera have fewer oral spines than the young zooecia (e.g., some species of *Pelmatopora*). In other cases the number of oral spines is the same in adult and young zooecia. There is no indication that the later species tend to have fewer oral spines than the earlier ones. In the following Table, 15 species are listed in which it has been possible to compare the numbers of oral spines in young and adult zooecia. It can be seen that, in the four genera represented, the number of oral spines is more variable in the young stages, and that reduction in number, if any, is commonly to four oral spines in the adult zooecia.

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[1] *Pelmatopora coryli*, *P. quadrivolucris*, *P. brydonei*, *P. marsupitorum*, *P. gregoryi*, *P. somptingensis* and *P. palmata*.

		Number of oral spines	
Horizon	Species	Young zooecia	Adult zooecia
M. cortestudinarium and *M. cor-anguinum* Zones	*Lagynopora lagena*	4, 5 or 6	4
M. cor-anguinum Zone	*L. birlingensis*	4	4
	L. praecursor	6	4
Marsupites Zone	*L. ollula*	6 or 7	4 or 5
O. pilula Zone	*L. urceolus*	5 or 6	4
	L. vasculum	4, 5 or 6	4
O. pilula and *B. mucronata* Zones	*L. amphora*	6	4
G. [*A.*] *quadrata* Zone	*L. ampulla*	5	4
	L. furcifera	5 or 6	4
Marsupites and *G.* [*A.*]*quadrata* Zones	*Hexacanthopora sexspinosa*	6 or 7	4, 5 or 6
O. pilula and *G.* [*A.*] *quadrata* Zones	*Leptocheilopora filliozati*	4, 5 or 6	4
B. mucronata Zone and *O. lunata* Chalk	*L. vulnerata*	7	7
B. mucronata Zone and Maastrichtian	*L. magna*	4	4
B. mucronata Zone and *O. lunata* Chalk	*Castanopora castanea*	4	4
	C. dibleyi	4 or 5	4 or 5

Lang (1921 : xliv) has stated that the oral spines " are primarily six in number " and that " In most families of Cretaceous Cribrimorphs the primary six apertural [oral] spines have been reduced to four ". He also mentioned a number of genera and species as not showing this tendency. From the exceptions mentioned by Lang, and from the evidence of the present work, it becomes difficult to recognize a general reduction in the number of the oral spines. The most that may be said is that some species of some genera show a variable reduction in the number of oral spines, others show no reduction, but none shows an increase.

ORAL SHIELDS. Accumulation of secondary calcareous tissue round the orifice may conceal the oral spines or they may form a visible part of a distal or proximal oral shield. Occasionally, as in the species of *Pelmatopora* with enlarged distal oral spines, the space between the spines may be filled with secondary tissue forming a small distal oral shield. More frequently, as in *Lagynopora*, the proximal-lateral pair of oral spines fuse with the bifurcated median process of the apertural bar thus forming a prominent " Y "-shaped proximal oral shield (Text-fig. 6*p*, *q*). In *Ubaghsia* the proximal-lateral oral spines may be enlarged, but otherwise unmodified, and fused on to the distal side of large lateral oral avicularia. Lang (1921 : xlv) mentioned other kinds of proximal and distal oral shields in which the oral spines may be involved, but these are not found in the genera described here. In genera with prominent hyperstomial ovicells the distal pair of oral spines often flank the entrance to the ovicell ; in some cases they appear to be displaced by it (e.g., Text-fig. 67—*Pelmatopora fecampensis*). A projecting distal oral shield may be formed in species with endozooecial ovicells. In these the space between the distal oral spines may be filled with secondary calcareous tissue (e.g., Text-fig. 89—*P. gregoryi*).

INTERZOOECIAL SECONDARY TISSUE. Lang has pointed out (1922 : 4) that the absence or extreme scarcity of interzooecial secondary tissue may be a useful diagnostic character. Many of the genera he described (1921) are devoid of it, and in the present material, it is absent in *Lagynopora*, *Hexacanthopora*, *Leptocheilopora* and *Aeolopora*.

When interzooecial tissue is present it may be very variable in amount. In the Pelmatoporidae, for example, a few genera, such as *Castanopora*, lack it, but in others, such as *Pnictopora* (Lang, 1922 : 145) the characters of the zooecia are almost totally concealed by it. *Pelmatopora* provides a good example of the extreme variation in amounts of secondary tissue which may be present in different species of the same genus and in different specimens of the same species. Thus in *P. calceata* there is no interzooecial secondary tissue ; in *P. crepidaria* it is only very slightly developed near the orifices ; and in *P. solearis* it may occur in contour-like ridges between the zooecia or it may be abundant, filling the interzooecial valleys. Other species of *Pelmatopora* may have extremely variable amounts of interzooecial secondary tissue, but it is generally abundant, either filling the interzooecial valleys or standing up as irregular ridges above the general level of the frontal shields.

The amounts of interzooecial tissue vary so widely that it is not a character which is useful for specific differentiation. Thus, although Lang (1922 : 319) separated *P. collium* [= *P. gregoryi*] from *P. saltdeanensis* [= *P. gregoryi*] solely on its supposedly greater accumulation in the former, the two species are alike in other characters and are here regarded as synonymous.

Apparently there is a tendency, seen in some young zoaria, for interzooecial tissue to be concentrated near the orifices in the early stages of its accumulation. In later stages, if it is at all abundant, it is fairly evenly distributed in the interzooecial valleys. Its continued accumulation, spreading out from the adult parts of a zoarium, may almost obscure the young zooecia. The ancestrula is often thus covered.

In the early stages of zoarial growth, before deposition of interzooecial tissue is complete, the gymnocysts of the zooecia may remain locally exposed. As accumulation continues, irregular openings or lacunae are maintained. These expose tissue which was deposited earlier or, occasionally, small areas of the gymnocyst may remain visible.

Lang (1921, text-figs. 7–9) has summarized three stages in the accumulation of interzooecial secondary tissue. It is difficult to be certain whether the tissue is first deposited in a narrow band round the gymnocyst as Lang has shown (text-fig. 7). In the material described here, the interzooecial tissue is apparently not deposited in a narrow ridge near the edge of the gymnocyst, but in a thin layer spreading from isolated points in the lowest parts of the interzooecial furrows. Subsequently, as shown by Lang (text-figs. 8, 9), lacunae remain in the accumulating tissue, but are gradually eliminated as it is built up into irregular interzooecial ridges.

General upgrowth of interzooecial tissue may contribute to the formation of a tertiary frontal wall (p. 33).

AVICULARIA. Workers on Recent and Tertiary cheilostome Polyzoa usually distinguish two main types of avicularia: (*a*) " adventitious " forms which occupy various positions on the outside walls of normal zooecia, and (*b*) " vicarious " or " interzooecial " forms which occur in series with normal zooecia. The terms " interzooecial " and " vicarious " are usually regarded as interchangeable.

In the Cretaceous cribrimorph Polyzoa, however, I distinguish between interzooecial and vicarious avicularia. The former are usually much smaller than the zooecia which they accompany and they do not occupy positions which would usually contain normal zooecia. The latter are often as large as, or larger than, the zooecia with which they occur, and occupy spaces which would otherwise be taken up by normal zooecia (Text-fig. 10*a*).

Adventitious avicularia are rare in the Cretaceous cribrimorphs. Lang (1921 : 166) has recorded distal adventitious avicularia in *Monoceratopora*. In the material described here, larger, apparently adventitious, distal avicularia occur in *Castanopora armata* sp. nov. (Text-fig. 103).

Vicarious avicularia are also infrequent in the Cretaceous cribrimorph Polyzoa. Some zoaria of *Leptocheilopora tenuilabrosa* (Pl. 7 ; Text-figs. 47, 48) possess very distinctive, large, spatulate, costate vicarious avicularia with distal apertural spines. Levinsen (1907 : 155, pl. opp. p. 160, figs. 1, 1*b*, 1*c*) has recorded large, spatulate, vicarious avicularia of a more usual type in *Castanopora* [*Cribrilina*] *labiata* (Text-fig. 10*b*).

Interzooecial avicularia occur very commonly in many genera of the Cretaceous cribrimorphs. They vary considerably in size, shape, number and position, and they may be directed distally, proximally, or variously. *Pelmatopora* affords a good example of the variation in detail which may occur in the interzooecial avicularia of one genus (Text-fig. 10*c–g*) and within a given species of one genus (Text-fig. 98*a–f*—*P. somptingensis*).

The shape of interzooecial avicularia is easily modified by wear. Sharply pointed rostra, which occur in various species of *Pelmatopora* and *Castanopora*, are often removed by wear leaving an apparently oval avicularian aperture. It may thus be misleading to record as oval the avicularia of species of which only one or very few specimens are available. This may be so in the case of *Pelmatopora calceata*. Similarly the transverse bar which may divide the rostrum of an avicularian aperture from the proximal portion is often broken, and it is difficult to decide whether the remaining lateral constrictions are the broken ends of such a transverse bar or true condyles on which the mandible was hinged (Text-fig. 10*h*). Interzooecial avicularia are often raised on fairly stout stalks, as in *Pelmatopora somptingensis* (Text-fig. 98*a*, *b*). In avicularia of this type, very little wear can remove the rostrum completely and reduce the visible structure to an oval cross-section of the stalk.

Where the avicularia are paired, one on either side of an orifice, they are often secondarily thickened and raised on very stout stalks which may fuse above the orifice, forming part of the proximal oral shield. This structure is well developed in *Ubaghsia ranunculus* (Text-fig. 117) and in other species of the same genus. Occasionally, as in *Haplocephalopora* (Lang, 1922 : 94), the avicularia may be very small and completely raised on the rim of a secondary tubular orifice.

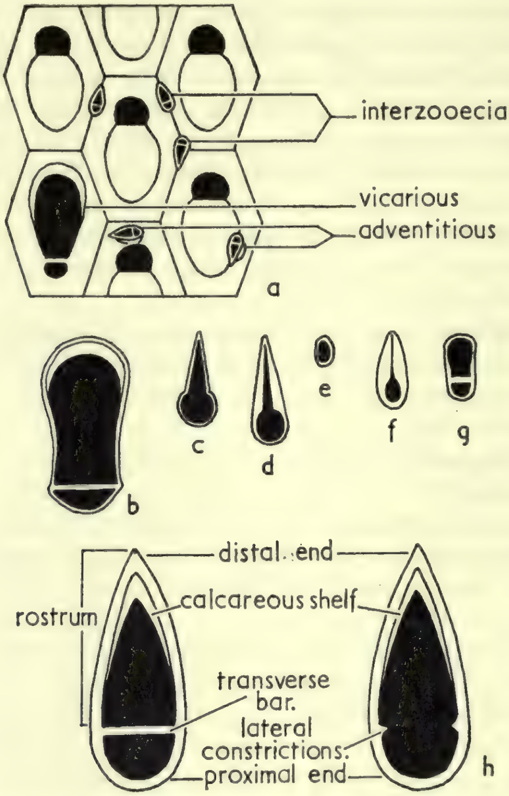

FIG. 10. Types of avicularia in Cretaceous cribrimorph Polyzoa.
a, Diagram showing the occurrence of the three main types. *b*, Vicarious avicularium of *Castanopora labiata* (Levinsen). *c–g*, Interzooecial avicularia of *Pelmatopora*, (*c*) *P. gregoryi*, (*d*) *P. somptingensis*, (*e*) *P. calceata*, (*f*, *g*) *P. marsupitorum*. *h*, General terminology of avicularia.

In species with abundant interzooecial tissue the avicularia may be almost immersed, and it becomes difficult to decide whether they are interzooecial or adventitious. Judging from the avicularia of species which lack interzooecial tissue the great majority appear to be truly interzooecial rather than adventitious. Waters (1923) has observed that Lang's text-figures of Cretaceous cribrimorph Polyzoa (1921 ; 1922) give the impression that most avicularia grow out of parts of gymnocysts of the zooecia, but that in his plates Lang has not shown this relationship. There is no indication that the majority of avicularia are adventitious.

Waters (1923) has also pointed out that there is great variation in the avicularia of some Recent cheilostomatous Polyzoa, and that there are genera, and even species, in which they are sometimes present and sometimes not. It has already been mentioned that in the Cretaceous cribrimorphs there is considerable variation in the interzooecial avicularia, but provided only well-preserved material is used and that avicularian characters are considered in relation to all other available features, the avicularia are certainly of value for differentiating species.

In some species the avicularia are always distally pointed and directed and paired near the orifices, while in others they may have a noticeably sporadic distribution and be variously directed. Avicularia of two or more distinct sizes may be present, as in *Hexacanthopora sexspinosa*. In the material described here the general characters of the avicularia of a given genus are fairly constant although the detailed characters may vary. Thus, in *Leptocheilopora*, apart from the large vicarious avicularia of *L. tenuilabrosa*, avicularia are absent. Those of *Lagynopora* are commonly very large and oval with lateral constrictions. In *Castanopora* they are usually long and pointed with somewhat spatulate rostra and often with transverse bars; in *Pelmatopora* the unworn avicularia generally have pointed rostra and often lack transverse bars.

The " secondary aviculoecia [avicularia] ", which Lang described as occurring in the more complex species of *Pelmatopora*, are modified oral spines. The structures have been discussed already (p. 38).

In the interzooecial avicularia of the material described here no example has been found in which minute spines are present on the distal margin of the avicularian aperture.

HETEROZOOECIA OTHER THAN AVICULARIA. These are apparently rare in the Cretaceous cribrimorph Polyzoa. In some species of *Pliophloea*, Lang (1921 : 174) has recorded interzooecial " swollen and hollow " tissue with small round pores and has suggested that the structures are " cenoecia " [kenozooecia]. In the present work, one specimen of *Aelopora distincta*, D.40658, was found to have clusters of very small, convex, smooth heterozooecia with large oval apertures on their upper surfaces (Pl. 1, fig. 5). These structures may be kenozooecia. Heterozooecia other than avicularia have not been found in the other genera and species studied.

OVICELLS. I agree entirely with the remarks made by Brown (1952 : 36) in a general discussion on the ovicells of the Cheilostomata. The present study shows that his remarks are completely applicable to the ovicells of Cretaceous cribrimorph Polyzoa.

Brown stated " In the majority of the Cheilostomata the ovicells appear as globular distal chambers sometimes resting lightly on and sometimes completely immersed in and covered by the frontal wall of the distal zooecium. Gradations between these two forms can be traced and no distinct boundary can be defined between the first or *hyperstomial* type (Text-fig. 11*a*), and the second or *entozooecial* [endozooecial] type (Text-fig. 11*b*). In fact, Silén (1944) has shown that in the Anasca there is essentially no difference between these two forms so far as their structure is concerned, and I have no doubt that the same remarks will be found to apply to those ovicells of the Ascophora which are of the same type. . . . Thus it appears impossible to sustain the view of some workers that the difference between " hyperstomial " and " entozooecial " ovicells can be used to subdivide not only genera but also families. . . . However, the terms are undoubtedly useful for descriptive purposes . . . ".

The examples given by Brown of the occurrence of both types of ovicell in species of the same genus and of the use of the two forms for subdivision of families can be paralleled by examples from the Cretaceous cribimorph Polyzoa. In *Pelmatopora* the globular ovicells may be external, as in *P. fecampensis* (Text-figs. 66–68), or partly concealed by the wall of the distal zooecium, as in *P. quadrata* (Text-fig. 64), or completely concealed, producing externally only a distal transverse shelf over the orifice, as in *P. marsupitorum* (Text-fig. 82), *P. somptingensis* (Text-fig. 99*a*, *b*) and *P. gregoryi* (Text-fig. 89). Lang (1921 : 4–6) has used the two types of ovicells to separate into two major groups the eleven families which he recognized in the Cretaceous cribrimorphs. One group with four families, including his Pelmatoporidae, he diagnosed as having endozooecial ovicells ; the remaining families he grouped together as having hyperstomial ovicells. Lang's statement (1921 : xxxv) that " the ovicell is of the same type throughout any given family of Cretaceous Cribrimorphs " is incorrect.

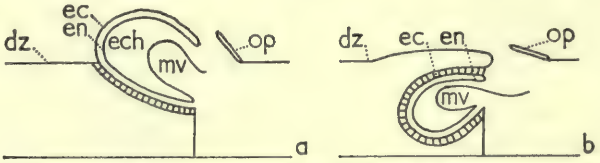

FIG. 11. Two types of ovicell in Cretaceous cribrimorph Polyzoa.
a, Hyperstomial. *b*, Endozooecial. *dz*, distal zooecium ; *ec*, ectooecium ; *ech*, brood chamber ; *en*, endooecium ; *mv*, median vesicle ; *op*, operculum. (After Harmer, 1926, text-fig. 1, and Brown, 1952, text-fig. 5.)

Following general usage (e.g. Brown, 1952 : 37) the outer and inner layers which compose the wall of the ovicell are termed " ectooecium " and " endooecium " respectively—" endooecium " is used in the present work as an alternative to " entooecium ".

In the hyperstomial ovicells in the present material the endooecium is apparently always smooth and complete. The ectooecium may be complete, or marginal with a median-proximal fenestra which exposes part of the endooecium. The ectooecium is often smooth, but diagonal and median ridges may be present, or it may be costate as in *Leptocheilopora tenuilabrosa* (Text-figs. 46, 47), or corrugated as in some specimens of *Aeolopora distincta* (Text-fig. 16). The upper margin of the opening of the ovicell may have a distinct labellum bounded by lateral slits, as in *Aeolopora*, or it may be entire as in the majority of genera and species. The opening of the ovicell is frequently flanked by a pair of oral spines, but equally often these may be obscured by the growth of the ovicell. Occasionally the growth of hyperstomial ovicells may displace the oral spines—this has apparently happened in some specimens of *Pelmatopora fecampensis*.

The presence of endozooecial ovicells is often completely concealed by interzooecial secondary tissue. Endozooecial ovicells may, however, produce a distal oral shield by the development of a distal transverse shelf filling the space between the distal pair of oral spines.

Other types of ovicell have been distinguished by Levinsen (1909), Canu & Bassler (1920), Brown (1952) and by other authors. In the material studied here I have seen only hyperstomial and endozooecial types.

YOUNG ZOOECIA AND ANCESTRULAE. Only two generalizations seem to be true of the young zooecia of all the Cretaceous cribrimorph Polyzoa. They are always smaller than the adult zooecia, and in any given zoarium the young zooecia never possess fewer oral spines than the adult zooecia.

The general characters of young zooecia, compared with the equivalent characters of the adult zooecia in any given zoarium, may be summarized briefly as follows:

(1) Size and shape of zooecia	Always smaller, but equally variable in shape.
(2) Extent of gymnocyst	Often more widely exposed, due partly to the general absence of interzooecial secondary tissue.
(3) Frontal shield	Often apparently more arched, again partly due to the absence of interzooecial secondary tissue.
(4) Number of costae	Very commonly less, but occasionally the same or more.
(5) Number of pelmata and lateral costal fusions	Very commonly less, but may be the same.
(6) Median area of fusion	Often narrower, but may be relatively as wide.
(7) Apertural bar	Usually simpler, lacking secondary modifications such as median processes or extra tissue.
(8) Primary orifice	Always smaller and usually the same shape, but liable to exhibit the same degree of variation in relative *hr* : *lr* values.
(9) Number of oral spines	Often greater or the same, but never less.
(10) Interzooecial secondary tissue	Commonly absent or scanty.
(11) Avicularia	Usually smaller and sporadic, but otherwise similar.

The majority of these remarks could be applied to the ancestrula of any given zoarium when it is compared with the young or adult zooecia.

Measurements

In each species studied, measurements are given where possible for the ancestrula, young and adult non-ovicelled zooecia and avicularia of parts of zoaria where normal growth appears to have taken place. It has been pointed out already (p. 24) that zooecial size may vary so greatly, often within a single zoarium, that in the absence of more definite characters it should seldom be used as a basis for differentiating species. On the other hand, the length and breadth of the orifice in a given species are often constant within a very small range and when considered in relation to all other available characters are often of value for specific differentiation.

The margins of the primary orifice are well defined and it is possible to make accurate measurements. In contrast, measurement of the zooecia is often made difficult by the fact that the distal and proximal walls may slope, and by the accumulation of interzooecial secondary tissue which obscures the true zooecial boundaries.

The following abbreviations are used in the present work :

Lz = length of zooecium.
lz = width of zooecium.
hr = length of orifice.
lr = width of orifice.
Lc = length of caudae.
lc = width of caudae.

The first two abbreviations are also used for the length and width of avicularia. The last two are used in the description of *Andriopora major* sp. nov. (p. 268).

Terminology

Brown (1952 : 32) has already commented on the large number of new terms which Lang (1913–19 ; 1921 : xxvi–li) introduced in his studies on the Cretaceous cribrimorphs to describe the " skeleton as distinguished from the tissue which secretes it ". I agree that there is no need in practice for such a complete duplicate terminology, and accordingly follow the general usage of modern zoologists, although I retain a few of Lang's terms such as "apertural bar". See also Lagaaij (1952 : 12).

ADULT ZOOECIA. See Zooecia.

ANCESTRULA. The first zooecium of a zoarium, formed by the metamorphosis of the larva.

APERTURAL BAR. Transverse proximal margin of the orifice formed by the fusion of the most distal pair of costae—symmetrical in all but the earliest Cretaceous cribrimorph Polyzoa.

APERTURE. The opening occupied in life by the frontal membrane. Used loosely by earlier workers and by Lang in the sense of the term " orifice " as defined here.

AVICULARIA. Heterozooecia provided in life with a powerful musculature producing movement in a mandible. They may be (a) *adventitious*—occupying various positions on the external walls of normal zooecia ; (b) *vicarious*—as large as, or larger than, the zooecia with which they occur, and occurring in positions usually occupied by normal zooecia ; or (c) *interzooecial*—usually much smaller than the zooecia which they accompany, not occupying positions which would usually contain normal zooecia.

CAUDAE. Elongate, narrow, tubular, proximal part of the gymnocyst in some uniserial genera.

COMMUNICATION PORES. Pores perforating the walls separating two zooecia (see also *dietellae*). [Syn., *septulum* (pl., *septula*)—a single small pore. Some of the large, single communication pores which occur in some genera of Cretaceous cribrimorph Polyzoa may have contained *multiporous septular discs* or thin disc-like structures with numerous small pores.]

CONDYLES. The tooth-like pivots of the operculum or the mandible.

COSTAE. [Syn., *costulae.*] Modified marginal spines, overarching the frontal membrane and forming the frontal shield in cribrimorph Polyzoa.

CRYPTOCYST. A more or less horizontal calcareous lamina on the basal side of the frontal membrane developed from the edge of the gymnocyst, but not completely subdividing the body-cavity.

DIETELLAE. Small enclosed spaces at the base of the distal and distal-lateral walls of the zooecia of certain Cheilostomata, and connected with the zooecia by communication pores.

DISTAL. The portions of a structure on the side away from the origin of growth or from the ancestrula.

DORSAL. The side of a zooecium opposite that composed of the frontal shield and orifice, or the side of a zoarium opposite that bearing the apertures [syn., *back, reverse*].

ECTOOECIUM. Outer layer of the ovicell wall.

ENDOOECIUM. Inner layer of the ovicell wall [syn., *Entooecium*].

ENDOZOOECIAL. Type of ovicell which may be completely immersed in and covered by the frontal wall of the distally adjacent zooecium, while opening into the vestibular arch [syn., *Entozooecial*].

FENESTRA. Uncalcified area in the ectooecium of an ovicell through which the endooecium is exposed.

FRONTAL MEMBRANE. Uncalcified part of the primary frontal wall—a chitinous membrane covering the aperture in life.

FRONTAL SHIELD. The secondary frontal wall in cribrimorph Polyzoa, formed above the aperture by the over-arching and fused costae.

FRONTAL WALL. Chitinous or calcareous cover of the ventral surface of the zooecia. In the cribrimorph Polyzoa it may be (a) *primary*—consisting of the calcareous gymnocyst, and in life of the chitinous frontal membrane, (b) *secondary*—formed by the frontal shield, or (c) *tertiary*—formed by an upgrowth and spread of secondary calcareous tissue above the primary and secondary frontal walls.

GYMNOCYST. The part of the frontal wall which lies between the aperture and the upper edges of the vertical zooecial walls—the calcified part of the primary frontal wall : it is usually most developed on the proximal side of the aperture.

HETEROZOOECIA. Modified zooecia either (*a*) lacking a polypide, or with only a vestige of one, but provided with a musculature, as in avicularia, or (*b*) without polypide or a musculature, as in kenozooecia.

HYPERSTOMIAL. Type of ovicell which rests on or indents the frontal wall of the distally adjacent zooecium.

INTERCOSTAL SPACES. Openings between the costae—they may be (*a*) single, long, slit-like spaces, or (*b*) subdivided into a series of smaller openings by lateral costal fusions. [Syn., *lacunae* of workers on Recent Polyzoa.]

INTERZOOECIAL. Term applied to any structure developed between zooecia of adjacent series, hence " interzooecial secondary tissue " is calcareous tissue accumulated between zooecia in the interzooecial valleys.

KENOZOOECIA. See Heterozooecia.

LABELLUM. The free tongue of the descending lamina of the ovicell.

LACUNAE. Irregular openings in the interzooecial secondary tissue.

LAMINA PERISTOMICA. Term introduced by Jullien and used by Lang, and here as synonymous with " tertiary frontal wall "—see Frontal Wall.

LATERAL COSTAL FUSIONS. Hollow cylindrical, lateral fusions between adjacent costae, usually arising at the levels of lumen pores. [Lang referred to the outermost lateral costal fusions as " primary ", and to the successive inner ones as " secondary, tertiary ", etc.]

LATERAL SLITS. The pair of slits at the sides of the labellum in some ovicells.

LUMEN LINE. Clear, membranous, median line seen along the upper surface of the costae in some Recent Cribrilinidae.

LUMEN PORES. Uncalcified, small, round, membranous areas on the upper surface of costae in some Recent Cribrilinidae. Lang's *pelmata* and *pelmatidia* of Cretaceous cribrimorph Polyzoa are lumen pores.

MANDIBLE. The triangular or rounded chitinous or calcareous structure which closes the orifice in the avicularium. Not preserved in the material studied here.

MARGINAL SPINES. Spines, other than oral spines, which surround the aperture. Modified as costae in the Cretaceous cribrimorph Polyzoa.

MEASUREMENTS. See p. 45.

MEDIAN AREA OF FUSION. The imperforate area formed by the fusion of the inner ends of the costae, which extends laterally from the mid-line of the frontal shield and which is bounded by the innermost intercostal spaces.

MEDIAN PROCESS. Median distal prolongation of the apertural bar. It may be a single, more or less pointed process, or it may bifurcate and fuse with the proximal pair of oral spines.

MULTIPOROUS SEPTULAR DISCS. See Communication Pores.

OPERCULUM. Chitinous or calcareous lamina, generally semicircular in shape, closing the orifice of the zooecium.

OPESIA. The opening into the body cavity which remains after development of the cryptocyst. In the Cretaceous cribrimorph Polyzoa it usually coincides with the aperture.

ORAL AVICULARIA. Avicularia which are associated with the orifice. In the Cretaceous cribrimorph Polyzoa a pair of avicularia, termed " lateral oral avicularia ", may occur one on either side of the orifice.

ORAL SHELF. The flattened rim round the distal and lateral margins of the orifice on which the operculum or mandible rests.

ORAL SHIELDS. Structures, other than a peristome, which develop round the primary orifice. They may form a *distal oral shield*, usually a marginal upgrowth produced by infilling of the space between distal oral spines with secondary tissue ; or a *proximal oral shield*, often formed by the fusion of the median process of the apertural bar with the proximal pair of oral spines, or by the thickening, upgrowth and fusion of lateral oral avicularia.

ORIFICE. The opening of the zooecium, covered by the operculum, for the extrusion of the polypide. It may be either (a) *primary* (the opening of the tentacular sheath covered by the operculum) leaving in the fossil state a well defined orifice with sharp limits and no marginal accumulation of secondary tissue, or (*b*) *secondary* when the primary orifice becomes surrounded by a peristome with a secondary orifice at its upper end. Lang introduced a series of terms such as "cribriline, normal, pliophloean" to describe various shapes of primary orifice (Text-fig. 7).

OVICELL. The distal, globular, structure in the fertile cheilostomatous zooecia, which serves as a brood-chamber to the developing larvae.

PELMA (pl., *pelmata*) and PELMATIDIUM (pl., *pelmatidia*). Large and small lumen pores respectively in the costae of Cretaceous cribrimorph Polyzoa. [Lang referred to the outermost pelmata and pelmatidia as " primary ", and successively to the inner ones as " secondary, tertiary " etc.] I have retained these two terms merely for convenience of reference but with no implication of acceptance of Lang's hypothesis of their origin (see p. 28).

PERISTOME. Tubular upgrowth of the rim of the primary orifice with the secondary orifice at its upper end.

POLYPIDE. The polyzoan animal with its tentacles placed in the interior of the zooecium.

PROXIMAL. The parts of a structure on the side near to the origin of growth or ancestrula.

ROSTRUM. That part of an avicularium which is distal to the transverse bar or condyles and on which the mandible rests.

SEPTULUM. See Communication Pores.

TRANSVERSE BAR. Narrow calcareous bar in some avicularia, on which the mandible hinges.

YOUNG ZOOECIA. See Zooecia.

ZOARIUM. The entire polyzoan colony.

ZOOECIUM. An individual member of the polyzoan colony. There is a difficulty in applying the terms " young " and " adult " to zooecia. They are here used as follows :

Young zooecia are those formed in the early stages of growth of the zoarium, after the ancestrula.

Adult zooecia are those formed in the late stages of growth of the zoarium.

I reject the following terms used by Lang, and indicate for each, after the colon, the term used by me :

Ancestroecium : ancestrula.

Apertural spines : oral spines. [Also used correctly by Lang for the spines which may occur on the distal edge of the aperture in some avicularia.]

Asty : zoarium.

Aviculoecium : avicularium.

Cenoecia : kenozooecia.

Costal spines : marginal spines.

Cribriline : a term used by Lang to describe a particular shape of primary orifice (see Orifice).

Epheboecium : adult zooecium.

Extraterminal front-wall : gymnocyst.

Fenestra : Lang used this term for openings in the calcareous tertiary frontal wall developed in some Cretaceous cribrimorph Polyzoa.

Gerontoecium : adult zooecium.

Heteroecia : heterozooecia.

Interoecial : interzooecial.

Intraterminal front-wall : frontal shield.

Lamina : cryptocyst.

Median lacunae : lacunae.

Neanoecia : young zooecia.

Normal : a term used by Lang to describe a particular shape of primary orifice (see Orifice).

Oecium : zooecium.

Orthoecium : zooecium.

Pliophloean : a term used by Lang to describe a particular shape or primary orifice (see Orifice).

Primary aperture : primary orifice.

Termen : a term used by Lang for the edge of the gymnocyst surrounding the aperture.

Note on the General Arrangement of the Systematics

The scheme adopted in the systematic sections of the present work is as follows.

Families and subfamilies. These are redefined where necessary. Synonymies precede the diagnoses and any changes suggested are discussed under remarks on the families or subfamilies involved.

Genera. The synonymy of each genus is given first, then the type species is cited and the genus diagnosed. Any changes are discussed under the remarks, and the stratigraphical range of the genus is given.

Species. After the synonymy the type of each species is cited in detail and its status given. When no type has been previously selected lectotypes are chosen in order to establish the species firmly. The diagnosis which follows is based on structures preserved in fossilization only, and the succeeding description is based on the characters of all material available to me. Where species are known from the literature only, or from photographs only, this is stated, and when the systematic position of a species is uncertain on this account, the species is listed as such and is not included in the general systematic assessment. Measurements are given where possible, and then general remarks on each species.

The stratigraphical distribution is stated and all the specimens which have been examined are listed with full details of locality and horizon. Under the heading " Specimens " is listed all the appropriate material which is in the collections of the

Department of Palaeontology of the British Museum (Natural History), each specimen with its registration number prefaced by the letter " D ". Material in the collections of other institutions is listed under " Other Material ". This includes specimens from the R. M. Brydone Collection in the Sedgwick Museum, Cambridge, the registration numbers of which are prefaced by the letters " S.M., B.". Specimens from the collections in the Norwich Castle Museum are denoted by the letters " N.C.M.".

Unless otherwise stated all the specimens are from C. T. A. Gaster Collection.

VII. SYSTEMATIC DESCRIPTIONS

Phylum *POLYZOA*
Class ECTOPROCTA
Tribe GYMNOLAEMATA
Order CHEILOSTOMATA Busk, 1852
Sub-Order ANASCA Levinsen, 1909

Division CRIBRIMORPHA Harmer, 1926

Family Pelmatoporidae Lang, 1916*a*

1916*a*	Pelmatoporidae Lang, p. 83.	
1921	Pelmatoporidae Lang :	Lang, pp. 1, 6.
1922	Pelmatoporidae Lang :	Lang, pp. 1–394.
1923	Pelmatoporidae Lang :	Waters, pp. 547, 553.
1925*b*	Pelmatoporidae Lang :	Voigt, pp. 97, 98, 99.
1927	Pelmatoporidae Lang :	Canu & Bassler, p. 18.
1930	Pelmatoporidae Lang :	Voigt, pp. 537, 538.
1935	Pelmatoporidae Lang :	Bassler, p. 31.
1953	Pelmatoporidae Lang :	Bassler, pp. G23, G190.
1958	Pelmatoporidae Lang :	Didon, p. 82.

Diagnosis. Multiserial Cribrimorpha with one or more pelmata or pelmatidia on each costa.

Remarks. Lang (1921 : 1) has stated that " If ovicells are present in the Pelmatoporidae, they are endozooecial ". In his key to the families of Cretaceous cribrimorph Polyzoa (1921 : 4), he divided into two groups the eleven families he recognized : group A was diagnosed as having hyperstomial ovicells and no pelmata or pelmatidia, group B as having endozooecial ovicells with pelmata or pelmatidia generally present.

It is shown below that some genera of Lang's group A possess pelmata or pelmatidia, and that both hyperstomial and endozooecial ovicells occur in the Pelmatoporidae. Brown (1952 : 43), in a brief discussion of the Membraniporidae, has stated that " although other workers (Canu & Bassler, 1920 ; Osburn, 1940) have used the difference between hyperstomial and entozooecial [endozooecial] ovicells to distinguish families, this is a very unreliable criterion, especially in the light of Silén's researches (1944) into the nature of the reproductive processes of the Polyzoa " (see also p. 43). It is apparent that the same remarks apply to the Cretaceous cribrimorph Polyzoa. Ovicells are not used here to distinguish families.

Stratigraphical distribution. Turonian to Danian.

Subfamily Pelmatoporinae Lang, 1916*a*

1916*a* Castanoporinae Lang, pp. 83, 93.
1916*a* Pelmatoporinae Lang, pp. 84, 101.
1916*a* Andrioporinae Lang, p. 382 [*partim—Aeolopora* only].
1916*a* Lagynoporidae Lang, p. 393.
1916*a* Lagynoporinae Lang, p. 393.
1916*a* Leptocheiloporinae Lang, pp. 394, 396.
1919*d* Pelmatoporinae Lang : Lang, pp. 191–228.
1921 Castanoporinae Lang : Lang, pp. xxxv, xli, xliv, xlv, xlvii, l, li, and p. 1.
1921 Pelmatoporinae Lang : Lang, pp. xli, l, li.
1921 Lagynoporidae Lang : Lang, pp. 5, 42.
1921 Lagynoporinae Lang : Lang, pp. 5, 44.
1921 Leptocheiloporinae Lang : Lang, pp. 5, 68.
1921 Andrioporinae Lang : Lang, p. 86 [*partim—Aeolopora* only].
1922 Castanoporinae Lang : Lang, pp. 5, 7, 10, 15, 154.
1922 Pelmatoporinae Lang : Lang, p. 235.
1927 Andrioporidae Lang : Canu & Bassler, p. 17 [*partim—Aeolopora* only].
1927 Lagynoporidae Lang : Canu & Bassler, p. 17.
1930 Lagynoporidae Lang : Voigt, p. 495.
1935 Andrioporidae Lang : Bassler, p. 30 [*partim—Aeolopora* only].
1935 Lagynoporidae Lang : Bassler, p. 30.
1943 Lagynoporidae Lang : Gillard, p. 186.
1953 Lagynoporidae Lang : Bassler, p. G188.
1953 Andrioporidae Lang : Bassler, p. G189 [*partim—Aeolopora* only].
1953 Pelmatoporinae Lang : Bassler, p. G192.
1953 Castanoporinae Lang : Bassler, p. G192.

Diagnosis. Pelmatoporidae with small or large zooecia ; with unmodified, or, enlarged or branched oral spines ; with or without oral shields ; apertural bar with or without a median process ; pelmata or pelmatidia present, either with one boss-like pelmatidium, or with one or more pelmata or pelmatidia on each costa ; with or without lateral costal fusions ; with or without a tertiary front wall ; with or without avicularia (if present these may be either sporadic, small and rounded, or paired, large and distally pointed) ; ovicells endozooecial or hyperstomial.

Remarks. The genera of Cretaceous cribrimorph Polyzoa which are revised here were placed by Lang (1916*a* ; 1921 ; 1922) in five subfamilies. This arrangement may be summarized as follows :

Revised genera	Subfamilies of Lang
Castanopora *Rhiniopora* (= *Castanopora*) *Ubaghsia*	Placed in the Castanoporinae [Lang, 1922 : 154].
Pelmatopora *Batrachopora* (= *Ubaghsia*)	Placed in the Pelmatoporinae [Lang, 1922 : 235].
Lagynopora *Prodromopora* (= *Lagynopora*) *Hexacanthopora*	Placed in the Lagynoporinae[1] [Lang, 1921 : 44].
Leptocheilopora . . .	Placed in the Leptocheiloporinae[1] [Lang, 1921 : 68].
Aeolopora	Placed in the Andrioporinae [Lang, 1921 : 89].

[1] Lang (1921 : 5, 44) placed these two subfamilies in the Lagynoporidae.

No distinction can be made between the Castanoporinae and the Pelmatoporinae. In his key to the subfamilies of the Pelmatoporidae Lang (1922 : 17) diagnosed them as follows : (*a*) Castanoporinae are Pelmatoporidae in which " costae bear *pelmatidia*[1] of several orders with lateral costal fusions corresponding in number and position to the pelmatidia ", (*b*) Pelmatoporinae are Pelmatoporidae in which " costae bear each one or more *pelmata*,[2] and lateral costal fusions correspond in number and position to the pelmata ".

As it is not possible to distinguish clearly between pelmata and pelmatidia (see p. 30) the two subfamilies are not separable on the basis given by Lang, nor are there any other characters which clearly help to maintain the division.

All genera previously assigned by Lang to the Lagynoporinae, and *Leptocheilopora*, the only genus which he placed in the Leptocheiloporinae, have distinct pelmata or pelmatidia and thus belong to the family Pelmatoporidae, and, according to Lang's definitions of its subfamilies, can be placed only in the Pelmatoporinae. Thus the subfamilies Lagynoporinae and Leptocheiloporinae, and the family Lagynoporidae which comprises them, are all synonymous with the subfamily Pelmatoporinae.

Aeolopora possesses boss-like pelmatidia and consequently belongs to the family Pelmatoporidae and is excluded from the Andrioporinae which Lang (1921 : 86) diagnosed as lacking, on the costae, either " a median row of pores " or " a median slit ". Again, according to Lang's definitions of the subfamilies of the Pelmatoporidae, *Aeolopora* can be assigned only to the subfamily Pelmatoporinae.

Thus all the genera listed in the above table are here regarded as belonging to the Pelmatoporinae.

STRATIGRAPHICAL DISTRIBUTION. Turonian to Danian.

KEY TO THE GENERA OF THE PELMATOPORINAE REVISED HERE

(I) Pelmatoporinae lacking a tertiary front wall ; secondary orifice absent or only slightly developed.
  (A) Zooecia small ; a single boss-like pelmatidium at the inner end of each costa 1. ***AEOLOPORA*** Lang
  (B) Zooecia large ; one or more normal pelmata or pelmatidia on each costa.
    (1) Proximal oral shield well developed—formed by the bifurcation of the median process of the apertural bar and its fusion with the proximal pair of oral spines . . . . 2. ***LAGYNOPORA*** Lang
    (2) Proximal oral shield absent.
      (*a*) Median process of the apertural bar present and not bifurcated 3. ***HEXACANTHOPORA*** Lang
      (*b*) Median process of the apertural bar absent. 4. ***LEPTOCHEILOPORA*** Lang
        (i) Costae less numerous with fewer pelmata or pelmatidia and lateral costal fusions ; avicularia usually of one kind, either small, rounded and sporadic, where no distal oral shield is developed, or large, elongate, distally pointed and directed, paired where a slight distal oral shield is formed by the enlargement of the distal pair of oral spines . . . . 5. ***PELMATOPORA*** Lang
        (ii) Costae numerous with numerous pelmata or pelmatidia and lateral costal fusions ; avicularia large, variously directed, of one, two or three kinds . . . . . . 6. ***CASTANOPORA*** Lang
(II) Pelmatoporinae with a well-developed secondary orifice and a tertiary front wall 7. ***UBAGHSIA*** (Jullien)

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[1] My italics.

Twelve other genera were placed by Lang (1916*a*; 1922) in his subfamilies Castanoporinae and Pelmatoporinae.

In the Castanoporinae he included seven genera other than those revised here. Provisionally I use Lang's definitions of these seven genera to distinguish them from those revised. Thus, according to Lang (1922 : 158), *Carydiopora, Anornithopora, Hesperopora* and *Stichocados* are distinguished from the other genera here placed in the revised subfamily of the Pelmatoporinae by their small size and fewer costae; *Phrynopora* by its unusual type of " secondary aperture " [proximal oral shield]; and *Steginopora* and *Disteginopora* by their types of tertiary front walls.

Similarly, Lang (1922 : 240) included in his subfamily Pelmatoporinae *Decurtaria, Murinopsia, Sandalopora, Ichnopora* and *Pachydera.* Various characters of these five genera, particularly the types of oral shields which may be developed, distinguish them from other genera placed in the revised subfamily of the Pelmatoporinae.

Genus ***AEOLOPORA*** Lang

1916*a* *Aeolopora* Lang, pp. 383, 390.
1921 *Aeolopora* Lang: Lang, p. 158.
1924 *Aeolopora* Lang: Gaster, second of three tables opp. p. 110.
1927 *Aeolopora* Lang: Canu & Bassler, p. 23.
1930 *Aeolopora* Lang: Gaster, table opp. p. 340.
1930 *Aeolopora* Lang: Voigt, p. 498.
1935 *Aeolopora* Lang: Bassler, p. 43.
1953 *Aeolopora* Lang: Bassler, p. G189.

TYPE SPECIES (by original designation). *Aeolopora distincta* Lang, 1916*a* : 390. Senonian, zone of *M. cor-anguinum.* Upper Basildon, Berkshire.

EMENDED DIAGNOSIS. Small Pelmatoporinae with a single boss-like pelmatidium near the distal end of each costa; no lateral costal fusions; ovicells hyperstomial, prominent, with labellum and lateral slits.

REMARKS. As is mentioned below, the boss-like structure near the distal end of each costa, which is characteristic of the genus, is interpreted as an unusual form of pelmatidium.

Lang (1916*a* : 382, 383) originally diagnosed *Aeolopora* as a multiserial, encrusting, Andrioporine genus lacking a " secondary aperture " [orifice], but with the " median area of fusion surrounded by a ring of solid spines; [and with] apertural [oral] spines thickened ". This diagnosis remained almost unchanged in his subsequent key to the Andrioporine genera (1921 : 88, 89).

Lang (1921 : 160), in his remarks on *A. distincta,* stated that " at the margin of the median area of fusion each costa bears a bead, which, to judge from comparable instances, is the original constricted distal end of the costa, which has retreated from the mid-line." It has been possible, using a magnification of ×140, to see that the so-called " beads " are not solid but possess a minute central pore which apparently connects with the central hollow of the costa. The structure is therefore regarded as a pelmatidium with an unusually high rim.

Remarking on the genus *Aeolopora,* Lang (1921 : 158, 159) also stated that " A tendency to this arrangement [the development of ' solid spines or beads ' round the median area of fusion] has already been noticed in *Andriopora gasteri* . . . *Eucheilopora* . . . *Pancheilopora*, and again in the species *Andriopora gallica* and *A. frequens*." These species of *Andriopora* and all available specimens belonging to the other two genera have been examined for the feature mentioned. At the most, there is a tendency for irregular median ridges to form, but circlets of boss-like pelmatidia, or of " solid spines or beads ", are definitely not present.

The presence of pelmatidia in *Aeolopora* removes the genus from both the subfamily Andrioporinae Lang, 1916*a*, and the family Andrioporidae Lang, 1916*a*, and places it in the subfamily Pelmatoporinae. The boss-like pelmatidia particularly distinguish the genus, which is always small and lacks lateral costal fusions, but possesses frequent, prominent, hyperstomial ovicells.

In the key to the families of Cretaceous cribrimorph Polyzoa Lang (1921 : 4–6) made a basic division of all families into (*a*) those with hyperstomial ovicells but without pelmata or pelmatidia and (*b*) those with endozooecial ovicells and pelmata or pelmatidia. *Aeolopora* is clearly a genus which has distinct hyperstomial ovicells and pelmatidia, though the latter are of an unusual form. The wider classification of the families and subfamilies of some of the Cretaceous cribrimorph Polyzoa is discussed elsewhere (p. 52).

STRATIGRAPHICAL DISTRIBUTION. Senonian, lower part of zone of *M. cor-anguinum* to zone of *B. mucronata.*

Of the two species *A. distincta* and *A. nebulosa*, here regarded as composing the genus, the former is apparently more abundant in the Senonian of southern England, ranging from the lower part of the zone of *M. cor-anguinum* into the zone of G. [*A.*] *quadrata*, while the latter has been recorded only from the zone of G. [*A.*] *quadrata* (or its equivalent, see Voigt, 1930 : 498) and from that of *B. mucronata* in the Isle of Wight.

A. nebulosa is somewhat larger and more robust and may be regarded as a development from *A. distincta*. Apparently *A. nebulosa* occurs much less frequently.

KEY TO SPECIES OF *AEOLOPORA*

(A) *Aeolopora* with 10–16, often 11–13, costae ; apertural bar of variable thickness, with or without two distinct boss-like pelmatidia near the mid-line ; avicularia occasionally present ; ovicells hyperstomial with labella and lateral slits . . . 1. ***A. distincta*** Lang

(B) *Aeolopora* with larger zooecia ; usually 9–12 costae ; apertural bar constantly thickened and prominent with a small median process above two indistinct boss-like pelmatidia ; avicularia apparently absent ; ovicells hyperstomial, with small labella and lateral slits . . . . 2. ***A. nebulosa*** Lang

1. ***Aeolopora distincta*** Lang

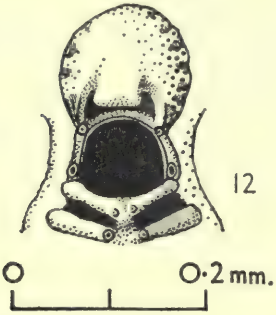
(Pl. 1 ; Pl. 2, figs. 1–7 ; Text-figs. 12–17)

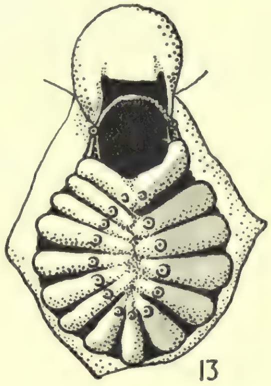
1916*a* *Aeolopora distincta* Lang, p. 390.
1916*a* *Aeolopora stellata* Lang, p. 390.
1921 *Aeolopora distincta* Lang : Lang, p. 159, pl. 5, fig. 4 ; text-fig. 75.
1921 *Aeolopora stellata* Lang : Lang, p. 161, text-fig. 76.
1924 *Aeolopora stellata* Lang : Gaster, second of three tables opp. p. 110.

1930 *Aeolopora stellata* Lang : Gaster, table opp. p. 340.
1935 *Aeolopora distincta* Lang : Bassler, p. 43.
1953 *Aeolopora distincta* Lang : Bassler, p. G189, text-fig. 143, 2.

Holotype. D.28062. Zoarial fragment encrusting a piece of echinoid test. Senonian, high in the zone of *M. cor-anguinum*. Upper Basildon, north-west of Pangbourne, Berkshire. L. Treacher Collection.

Emended diagnosis. *Aeolopora* with orifice of equal height and width, or hr exceeds lr very slightly ; oral spines 6, costae 10–16, but very often 11–13 only ; apertural bar of variable thickness with or without two distinct boss-like pelmatidia near the mid-line ; heterozooecia (? kenozooecia) occasionally present ; avicularia present ; ovicells abundant, hyperstomial, with labella and lateral slits.





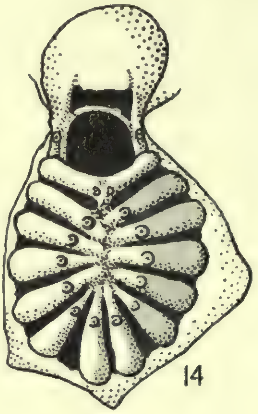


Fig. 12. *Aeolopora distincta* Lang, D.40599. Orifice and ovicell with complete ectooecium and well-formed labellum and lateral slits.

Fig. 13. *Aeolopora distincta* Lang, D.28062. Holotype. Ovicelled zooecium.

Fig. 14. *Aeolopora distincta* Lang, D.28911. Holotype of *A. stellata* Lang. Ovicelled zooecium.

Description. *Zoarium* encrusting, unilaminar. *Zooecia* closely placed, oval. *Orifice* small, distally rounded, the sides straight, or tending to diverge proximally, the proximal-lateral corners may be somewhat rounded, proximal margin straight to widely " V "-shaped. *Oral spines* 6, apparently secondarily thickened, but small, arranged on the distal-lateral margins and sides of the orifice, usually paired symmetrically. *Frontal shield* well arched. *Costae* variable from 10–16, but very often 11–13, fairly closely placed, widest at their proximal (outer) ends and tapered distally. Each costa bears near its distal (inner) end a small, prominent, boss-like *pelmatidium*.[1] There are no *lateral costal fusions*. The costae slope upwards to the pelmatidia and then flatten to join the *median area of fusion*, which is flat, of variable width, and may be occasionally absent. *Apertural bar* variable in thickness, often narrow, fairly straight or widely " V "-shaped, usually with, but sometimes apparently lacking, a pair of distinct boss-like pelmatidia near the mid-line. The apertural bar is never so consistently thickened as in *A. nebulosa*. *Gymnocyst* only slightly exposed. There is no *interzooecial secondary tissue*.

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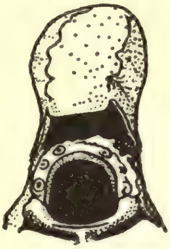
[1] The " bead or solid spine " of Lang (1921 : 161).



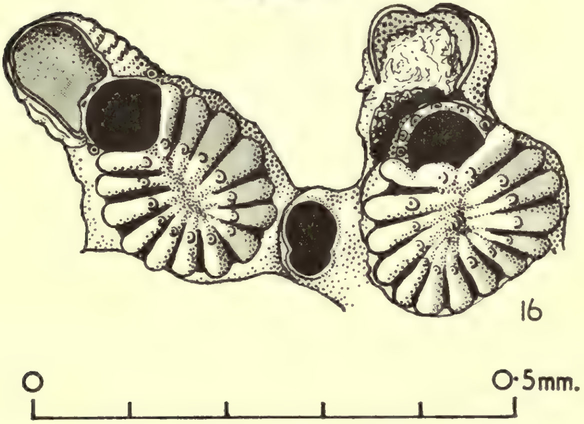


FIG. 15. *Aeolopora distincta* Lang, D.40578. Orifice and ovicell, the latter with a lateral growth of ectooecium.

FIG. 16. *Aeolopora distincta* Lang. D.40559. Two ovicelled zooecia and interzooecial avicularium. Both ovicells are damaged but that on the left shows the corrugated ectooecium.

Avicularia interzooecial, occurring infrequently in any zoarium, fairly large, oval, distally directed and with slight lateral constrictions (Text-fig. 16). In most zoaria avicularia are absent.

Heterozooecia (? kenozooecia) occasionally present, very small (one-fifth to one-quarter the size of the normal zooecia), convex, smooth, each with a large oval aperture on the upper surface, occurring singly or grouped in irregular clusters between the zooecia (seen only in D.40658).

Ovicells abundant, hyperstomial, prominent, globular, smooth, with a distinct *labellum* bounded by short *lateral slits*. The endooecium of the primary ovicell may be covered by a slightly corrugated ectooecium (Text-figs. 12, 15, 16). The ovicelled zooecia sometimes occur in linear series.

MEASUREMENTS. *Zooecia* Lz = 0·27 to 0·33 mm.
lz = 0·19 to 0·25 mm.
hr = 0·05 to 0·07 mm.
lr = 0·05 to 0·06 mm.
Avicularia Lz = 0·05 mm.
lz = 0·03 mm.

REMARKS. Lang (1916*a* : 390) originally referred two species, *A. distincta* Lang and *A. stellata* Lang, to *Aeolopora*, but the present revision shows that they are synonymous ; his later (1921) species, *A. nebulosa*, is clearly definable, however.

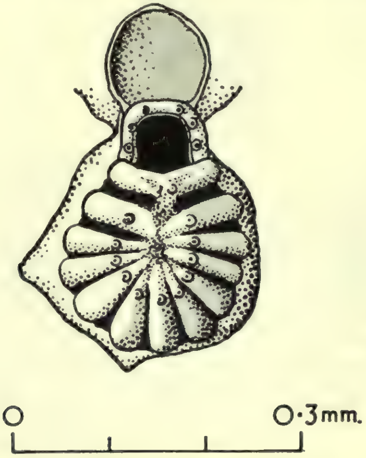


FIG. 17. *Aelopora distincta* Lang, D.40571. Zooecium, with very worn ovicell, showing arrangement of oral spine-bases.

A. distincta and *A. stellata* were separated primarily on the number of " beads surrounding the median area of fusion " and on the form of the apertural bar. All the available specimens of *Aeolopora*, labelled by Lang as belonging to these species, have been re-examined, and the results may be tabulated briefly as follows :

	Specimens assigned by Lang to *A. distincta*	Specimens assigned by Lang to *A. stellata*
Lz .	0·30 to 0·33 mm. .	0·27 to 0·32 mm.
lz .	0·20 to 0·25 mm. .	0·19 to 0·23 mm.
hr .	0·05 to 0·07 mm. .	0·06 mm.
lr .	0·05 to 0·06 mm. .	0·05 to 0·06 mm.
Number of costae .	10–16 (often 12 or 13)	11–15 (often 11 or 12)

As Lang indicated (1921 : 159, 161), the dimensions of the two species are virtually the same.

The apertural bar of *A. distincta*, according to Lang (1921 : 160), " is somewhat flattened in a vertical plane, and each of the costae of which it is composed retains the bead formed by its constricted distal end, and this takes its place in the ring of beads ". In contrast, he stated (p. 161), the apertural bar of *A. stellata* " is considerably flattened in a vertical plane, and, unlike the apertural bar of *A. distincta,* does not normally bear a median pair of beads ".

I have not found it possible to distinguish between the two by the form of the apertural bar. The structure is easily modified by wear, and is in itself variable both in the zooecia of a single zoarium and in those of different zoaria of each species recognized by Lang. The apertural bars of adjacent zooecia may be of varying thickness, and the boss-like pelmatidia, which are present near the mid-line, may or may not be distinct (cf. Text-figs. 13–16) : they are often visible in the specimens labelled by Lang *stellata* and are not, as he suggested, " not normally present ".

The number of boss-like pelmatidia necessarily varies with the number of costae, and, as is apparent from the above table, the range in number of costae of *A. stellata* is contained within that of *A. distincta.*

Thus the two species are regarded as synonymous, the name *distincta* being retained for them.

Many new specimens, ranging from the zone of *M. cor-anguinum* to that of *G.* [*A.*] *quadrata,* have been assigned to the species, and although much of this material has been measured it has not proved necessary to extend the ranges established in the re-examination of Lang's specimens. Many specimens show the details of the ovicell, particularly D.28062, D.28911, D.40578, D.40559 and D.40653. Heterozooecia are present in D.40658, (Pl. 1, fig. 5).

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum* to zone of *G.* [*A.*] *quadrata.*

SPECIMENS. D.28062. Holotype—see above.

D.28911. Holotype of *A. stellata* Lang, encrusting a fragment of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit 2 of Gaster, by reservoir, near Hill Barn, North Lancing, east of Worthing, Sussex.

D.21212–13. Two paratypes of *A. distincta* Lang. Horizon, locality and collection as for D.28056 and D.28052 respectively.

D.23326–28. Three paratypes of *A. distincta* Lang, D.23326–27 encrusting *Inoceramus* fragments, D.23328 encrusting a piece of echinoid test. Senonian, top of zone of *M. cor-anguinum.* Medical College Pit, Epsom, Surrey. F. Möckler Collection.

D.23950. Paratype of *A. distincta* Lang, six well-preserved zooecia encrusting a very small shell fragment. Horizon, locality and collection as for D.23326.

D.28052–55. Four paratypes of *A. distincta* Lang. Four or five incomplete zoaria encrusting one fragment of echinoid test [the fifth zoarial fragment numbered D.21213]. Senonian, zone of *M. cor-anguinum.* Upper Basildon, north-west of Pangbourne, Berkshire. L. Treacher Collection.

D.28056–61 and D.28063–66. Ten paratypes of *A. distincta* Lang. Ten of twelve incomplete zoaria encrusting one fragment of echinoid test [the other two zoarial fragments numbered D.21212 and D.28062—the latter the holotype]. Horizon, locality and collection as for the holotype.

D.28246. Paratype of *A. distincta* Lang, encrusting a fragment of *Inoceramus*. Senonian, zone of *M. cor-anguinum*, about 40 ft. from base of zone (20 ft. below the "strong *cor-anguinum* tabular" [flint band] of Whitaker and Rowe). Cliffs between Beltout and Birling Gap, west of Beachy Head, Sussex.

D.3248. Paratype of *A. stellata* Lang, encrusting a fragment of *Inoceramus*. Senonian, zone of *G.* [*A.*] *quadrata*. Romsey, south-west of Winchester, Hampshire. H. P. Blackmore Collection.

D.28918–21. Four paratypes of *A. stellata* Lang, encrusting fragments of echinoid tests. Horizon, locality and collection as for D.28911.

D.28965–66. Two paratypes of *A. stellata* Lang, encrusting one fragment of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 7 of Gaster, in Lambleys Lane, Sompting, south of Lambleys Barn, north of Upton Cottages, north-west of Sompting Church (just above the 200 ft. contour).

D.28986. Paratype of *A. stellata* Lang, encrusting a fragment of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 10 of Gaster, Western Pit, Charman Dean, north of Broadwater, north of Worthing, Sussex.

D.29885. Incomplete zoarium labelled "?*A. stellata* Lang", encrusting a fragment of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs between last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.

D.29888. Specimen labelled "*A. distincta* Lang", encrusting a fragment of echinoid test. Senonian, zone of *M. cor-anguinum*. Coombs Pit, West Horsley, north-east of Guildford, Surrey.

D.29889–90. Two specimens labelled "*A. stellata* Lang", the former encrusting a fragment of *Ostrea*, the latter a fragment of *Inoceramus*. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 2 of Gaster—see D.28911.

D.29891. Specimen labelled "*A. stellata* Lang", encrusting a fragment of *Inoceramus*. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit 4 of Gaster. Western Pit, below Lancing Ring, west side of Boundstone Lane, north-east of Worthing, Sussex.

D.29892. Specimen labelled "*A. stellata* Lang", encrusting a fragment of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Locality and collection as for D.29885.

D.29893. Specimen labelled "*A. stellata* Lang", encrusting a fragment of echinoid test. Senonian, zone of *Marsupites testudinarius*, subzone of *Uintacrinus westphalicus*. Medical College Pit, Epsom, Surrey.

D.40555. Zoarial fragment encrusting part of a *Pelmatopora* zoarium. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 3 of Gaster, east pit at top of Boundstone Lane, North Lancing, near Worthing, Sussex.

D.40556. One of two incomplete zoaria encrusting a fragment of echinoid test [ancestrula present]. Horizon as for D.40555, Pit 4 of Gaster, western pit at top of Boundstone Lane, North Lancing, near Worthing, Sussex.

D.40559–61. Three incomplete zoaria—D.40559–60 encrusting the same *Inoceramus* fragment, D.40561 encrusting a piece of echinoid test. Horizon as for D.40555, Pit 2 of Gaster—see D.28911.

D.40562. Incomplete zoarium encrusting a small, whole valve of *Ostrea*. Horizon, locality and collection as for D.40555.

D.40563–80. Eighteen specimens, all encrusting fragments of echinoid tests. Two specimens—Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*, Pit 2 of Gaster (see D.28911—above), the rest from the subzone of *E. scutata* var. *depressula* of Section 113 of Gaster—cliffs between the last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.

D.40581–94. Fourteen specimens, all encrusting fragments of echinoid tests, except D.40581–83, D.40587–88 and D.40590–91 which encrust fragments of *Inoceramus*. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pits 2 and 4 of Gaster—see D.28911 and D.29891 respectively.

D.40595–98. Four specimens encrusting fragments of *Inoceramus*. Senonian, zone of *M. cor-anguinum* (less than 10 ft. below strong *cor-anguinum* tabular). Cliffs, Beltout, near Eastbourne, Sussex.

D.40599. Specimen encrusting a fragment of *Inoceramus*. Senonian, zone of *M. cor-anguinum*. Southern England—precise locality and collection unknown.

D.40600. Specimen encrusting a fragment of *Inoceramus*. Senonian, base of zone of *M. cor-anguinum* (about 20 ft. below the strong *cor-anguinum* tabular). Cliffs between Beltout and Birling Gap, west of Beachy Head, Sussex.

D.40601. Incomplete zoarium encrusting the same echinoid fragment as D.40556.

D.40602–05. Four specimens, D.40602–03 encrusting fragments of echinoid tests, D.40604–05 encrusting fragments of *Inoceramus*. Senonian, zone of *M. cor-anguinum* (*Trochiliopora* Bed). Cliffs, Seaford district, Sussex.

D.40606–18. Thirteen specimens, all encrusting echinoid fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 10 of Gaster, Charman Dean, near Worthing, Sussex.

D.40619. Specimen encrusting a fragment of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 24 of Gaster, Warningcamp Hill, Warningcamp, north-east of Arundel, Sussex.

D.40620–23. Four specimens encrusting fragments of echinoid tests. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 26 of Gaster, South Woodleighs Pit, east of gravel pit, north-east of Woodleighs Lodge, about half a mile west of Pit 24, Warningcamp, north-east of Arundel, Sussex.

D.40624–26.	Three specimens encrusting fragments of echinoid tests. Senonian, zone of *G.* [*A.*] *quadrata*. Locality, horizon and collection as for D.40606.
D.40627.	Specimen encrusting a fragment of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 2 of Gaster. Horizon, locality and collection as for D.28911.
D.41064.	Zoarial fragment encrusting a piece of *Ostrea* shell. Senonian, zone *O. pilula*, subzone of *E. scutata* var. *depressula*. Section 113 of Gaster, cliffs Rottingdean, Sussex.
D.40628.	Specimen encrusting a fragment of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Locality and collection as for D.40606.
D.40629–31.	Three specimens, encrusting fragments of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 12 of Gaster, large pit north of Pumping Station, top of Waterworks Lane, north-east of "The Warren", north of Broadwater and Worthing, Sussex.
D.40632–33.	Two specimens encrusting fragments of echinoid tests. Senonian, either lowest part of zone of *G.* [*A.*] *quadrata* or topmost part of zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 3 of Gaster, eastern pit at top of Boundstone Lane, south of Lancing Ring, north of Fir Croft, North Lancing, Sussex.
D.40634–36.	Three specimens, encrusting fragments of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 15 of Gaster, large pit about one-third of a mile south-south-east of Salvington Windmill, and north of Hill Cottages, Salvington, Sussex.
D.40637–44.	Eight specimens, all encrusting inner surfaces of fragments of echinoid tests. Senonian, zone of *G.* [*A.*] *quadrata*. South side of Pit 1143 of Brydone. Redhampton Limeworks Pit, Portsdown, Hampshire.
D.40645.	Specimen encrusting a fragment of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 16 of Gaster. Pit by main road, east of Swandean Isolation Hospital and half a mile south of Salvington Windmill, Durrington, Sussex.
D.40646–54.	Nine specimens, all encrusting fragments of echinoid tests. Horizon, locality and collection as for D.40606.
D.40655–57.	Three specimens, encrusting one fragment of echinoid test. Horizon, locality and collection as for D.40634.
D.40658.	Incomplete zoarium with heterozooecia, encrusting a fragment of echinoid test. Horizon, locality and collection as for D.28965.
D.38852.	Zoarial fragment encrusting an *Inoceramus*. Upper Chalk. Grove Park Road, Bury St. Edmonds, Suffolk. J. L. Gilbert Collection.

2. ***Aeolopora nebulosa*** Lang

(Pl. 2, figs. 8, 9; Text-figs. 18, 19)

1921 *Aeolopora nebulosa* Lang, p. 163, pl. 5, fig. 5; text-fig. 77.
1924 *Aeolopora nebulosa* Lang: Gaster, second of three tables opp. p. 110.
1930 *Aeolopora nebulosa* Lang: Voigt, pp. 498, 542, 560, pl. 27, fig. 1.

Holotype. D.29061. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 7 of Gaster, in Lambleys Lane, Sompting, south of Lambleys Barn, north of Upton Cottages, north-west of Sompting Church, just above the 200 ft. contour.

Emended diagnosis. *Aeolopora* with somewhat larger, more robust zooecia than those of *A. distincta*; orifice of equal height and width, or hr exceeds lr very slightly or vice versa; oral spines 6, considerably thickened; costae usually 9–12 (occasional adult zooecia may have 8 or 13); apertural bar prominent, considerably thickened, wide, its distal face nearly vertical, noticeably produced upwards in the mid-line, with or without two distinct boss-like pelmatidia; avicularia apparently absent; ovicells prominent, hyperstomial, with small labellae and lateral slits.

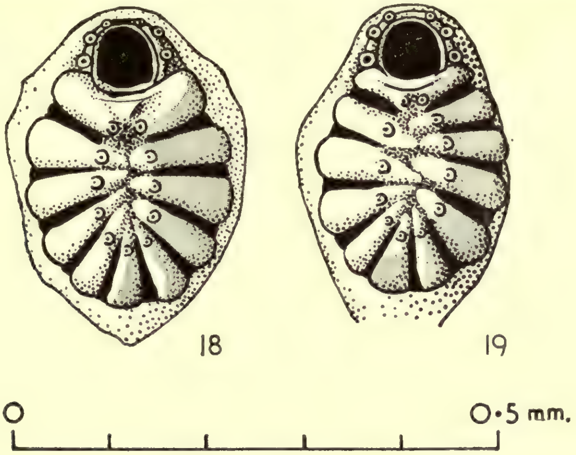


Fig. 18. *Aeolopora nebulosa* Lang, D.29061. Holotype. Zooecium with very thick apertural bar.

Fig. 19. *Aeolopora nebulosa* Lang, D.29061. Holotype. Zooecium with narrow apertural bar and well-developed oral spine bases.

Description. *Zoarium* encrusting, unilaminar. *Zooecia* closely placed, oval, somewhat larger than those of *A. distincta* and more robust. *Orifice* small, always distally rounded, the sides straight, proximal margin slightly curved. *Oral spines* 6, prominent, considerably thickened but otherwise unmodified, usually paired and evenly spaced. *Frontal shield* well arched. *Costae* thicker and more robust than in *A. distincta*, usually 9–12, but occasionally adult zooecia may possess only 8, and less frequently may have 13. The costae narrow inwards, and each bears a small, prominent, boss-like *pelmatidium* fairly close to its distal (inner) end. There are no *lateral costal fusions*. The outline of the distal extremity of each costa may often be traced in the *median area of fusion*, which is relatively flat, and usually narrower than in *A. distincta.* Outwards from the boss-like pelmatidia the costae slope down to meet the gymnocyst less steeply than in *A. distincta. Apertural bar* prominent, considerably thickened, wide or very wide, its distal face vertical, produced upwards in the mid-line to form a small *median process*. Beneath the median process and proximal to it, a pair of boss-like pelmatidia may or may not be distinct. The apertural bar is generally straighter than that of *A. distincta*. *Gymnocyst* only slightly exposed. There is no *interzooecial secondary tissue*.

Avicularia apparently absent. *Heterozooecia* not seen. *Ovicells* prominent, hyperstomial, globular, smooth with a small *labellum* and *lateral slits*. If an ectooecium is present it is not corrugated—as may be the case with *A. distincta*.

MEASUREMENTS. *Zooecia* Lz = 0·30 to 0·40 mm.
lz = 0·20 to 0·30 mm.
hr = 0·06 to 0·08 mm.
lr = 0·06 to 0·07 mm.

REMARKS. The dimensions given by Lang for *A. nebulosa* (Lz = about 0·40 mm. and lz = about 0·30 mm.) were maximum measurements. It is, however, apparent that *A. nebulosa* may be distinguished from *A. distincta* by its rather larger size, its more robust appearance, its definitely thicker oral spines, its thicker, and generally fewer costae, and its more constantly thickened apertural bar which may be very prominent (Text-figs. 18, 19). The labellum tends to be smaller than in *A. distincta*. Avicularia have not been seen in any of the specimens examined and their absence may again be of diagnostic value.

Lang (1921 : 163) described the apertural bar of *A. nebulosa* as " thick, flattened in a vertical plane, and produced medianly in a spine-like projection ". This median projection may not always be present and is never very marked; it is particularly prone to wear. The apertural bar of *A. distincta* also tends to be thickened medianly and this may occasionally produce a median projection. It is not true to describe the form of the orifice as " cribriline "[1] (Lang, 1921 : 163); the proximal-lateral constrictions characteristic of this type of orifice are not present.

Voigt (1930 : 498, pl. 27, fig. 1) very briefly recorded a specimen which he assigned to *A. nebulosa* Lang from the Mammillatensenon of Ifö, Sweden.

Specimens D.40660–65, from the zone of *B. mucronata* of the Isle of Wight extend the upward range of the species. The holotype, D.29061, is from the zone of *G.* [*A.*] *quadrata* of Sussex and the paratype specimens from the same horizon in Wiltshire. No specimens of *A. nebulosa* have been discovered as yet below this horizon. Much new material belonging to the genus, has been examined, but apart from the specimens from the zone of *B. mucronata* all have proved to belong to *A. distincta* Lang.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *G.* [*A.*] *quadrata* to zone of *B. mucronata*.

SPECIMENS. D.29061. Holotype—see above.

D.3251.	Paratype encrusting a fragment of ?echinoid test. [D.29052–53 are probably parts of the same specimen.] Senonian, zone of *G.* [*A.*] *quadrata*. East Harnham, south of Salisbury, Wiltshire. H. P. Blackmore Collection.

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[1] See Lang, 1921 : xlvii.

D.29052–53. Two paratypes [poorly preserved], encrusting. Horizon, locality and collection as for D.3251.

D.40660. Zoarial fragment, encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Pit 9 of Rowe, south of the Briary, between Alum Bay and Freshwater, Isle of Wight.

D.40661–65. Five incomplete zoaria, encrusting fragments of echinoid tests. Senonian, zone of *B. mucronata*. Pit 6 of Rowe, south of Newbarn, Afton Down, Isle of Wight.

Genus ***LAGYNOPORA*** Lang

?1874	*Lepralia* : Reuss, p. 129 [*partim*].
1877	*non Lepralia* : Novák, pp. 82, 93 [*partim*].
1889	*non Lepralia* : Fric, p. 90.
1893	*Cribrilina* : Vine, pp. 316, 336 [*partim*].
?1900*b*	*Cribrilina* : Canu, p. 445 [*partim*].
1904	*Cribrilina* : Jukes-Browne, p. 490 [*partim*].
1910	*Cribrilina* : Brydone, p. 391.
1916*a*	*Prodromopora* Lang, p. 394.
1916*a*	*Lagynopora* Lang, p. 394.
1921	*Lagynopora* : Lang, pp. lxi, xci–v, 52.
1921	*Prodromopora* : Lang, pp. lxiii, xciv, 50, 51.
1927	*Lagynopora* : Canu & Bassler, p. 17.
1927	*Prodromopora* : Canu & Bassler, p. 36.
1930	*Prodromopora* : Kühn, p. 65.
?1930	*Canupora* Kühn, p. 65.
1930	*Lagynopora* : Gaster, table opp. p. 340.
1930	*Lagynopora* : Voigt, pp. 495, 542, 560.
?1935	*Canupora* : Bassler, pp. 30, 64.
1935	*Prodromopora* : Bassler, pp. 30, 176.
1935	*Lagynopora* : Bassler, pp. 30, 135.
1949	*Lagynopora* : Voigt, pp. 36, 43, 44.
?1953	*Canupora* : Bassler, p. G188.
1953	*Prodromopora* : Bassler, p. G188.
1953	*Lagynopora* : Bassler, p. G188.
1958	*Lagynopora* : Didon, pp. 80, 84.

TYPE SPECIES. *Lagynopora lagena* Lang, 1916*a* : 395. Senonian, zone of *M. cortestudinarium* or zone of *M. cor-anguinum*. Chatham, Kent. W. Gamble Collection.

EMENDED DIAGNOSIS. Pelmatoporinae with a median process on the apertural bar which bifurcates and fuses with the proximal pair of oral spines producing a prominent oral shield ; avicularia usually present.

REMARKS. *Lagynopora* may be clearly distinguished from other genera of the Pelmatoporinae by its distinctive proximal oral shield. In specimens which have been worn the proximal shield may often be destroyed. Usually, however, a few of these structures survive. Also it is possible to infer their presence originally in worn zooecia by the form of the apertural bar, and, in contrast to those of *Hexacanthopora*, by the lengthened and enlarged proximal oral spines, originally fused to the median process.

Prodromopora Lang is synonymous with *Lagynopora*. Lang (1916*a* : 394 ; 1921 : 50) regarded the few, narrow, widely spaced costae and the slight median area of fusion in *Prodromopora* as generically significant. Other characters were recognized as similar to those of *Lagynopora*. The characters of the frontal shield are, however, of specific value only, and *Prodromopora praecursor* Lang is placed in *Lagynopora*.

Canupora prima Kühn (1930 : 65) is here provisionally referred to *Lagynopora* and is listed and described as a species of uncertain systematic position (p. 96). I exclude from this genus *Lepralia pediculus* Reuss, which Lang doubtfully referred to *Lagynopora* (see p. 95).

Excluding *Lagynopora*? *prima* (Kühn), 12 species are recognized, one of which, *L. pustulosa*, is new.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cortestudinarium* to zone of *B. mucronata* in England, zone of *G.* [*A.*] *quadrata* in Germany, and ?Danian in Austria.

KEY TO THE SPECIES OF *Lagynopora* LANG

- (I) *Lagynopora* with boss-like pelmata . . . . . . 1. ***L. pustulosa*** sp. nov.
- (II) *Lagynopora* in which the pelmata are minute pores.
  - (A) Distinct lateral costal fusions present . . . . 2. ***L. horsleyensis*** Lang
  - (B) No lateral costal fusions.
    - (1) Intercostal spaces wide, as long as the costae ; median area of fusion very slight ; costae narrow (11–14) . . . . . 3. ***L. praecursor*** (Lang)
    - (2) Intercostal spaces narrower, but still distinct and nearly as long as the costae.
      - (a) Zooecia small, Lz = 0·43 to 0·60 mm., lz = 0·25 to 0·37 mm.
        - (i) Costae 11–14 ; avicularia occasional, fairly large, oval 4. ***L. saltdeanensis*** Lang
        - (ii) Costae 17–18 ; avicularia abundant, small, oval 5. ***L. birlingensis*** Lang
      - (*b*) Zooecia large, Lz = 0·64 to 0·75 mm., lz = 0·37 to 0·50 mm. ; costae 13–17 ; frontal shield often with a median ridge . 6. ***L. amphora*** Lang
    - (3) Intercostal spaces limited to the outer margins of the frontal shield.
      - (*a*) Costae 12–14. . . . . 7. ***L. ampulla*** Lang
      - (*b*) Costae 20–23. . . . . 8. ***L. furcifera*** (Brydone)
    - (4) Intercostal spaces absent ; costae juxtaposed, outlined by furrows only.
      - (*a*) Zooecia small, Lz = 0·48 to 0·68 mm., lz = 0·35 to 0·51 mm.
        - (i) Costae 9–11 ; oral spines 4 or 5 ; avicularia of one kind, large, prominent, oval . . . . 9. ***L. ollula*** Lang
        - (ii) Costae 13–20 ; oral spines always 4 ; avicularia of two sizes 10. ***L. lagena*** Lang
      - (*b*) Zooecia large, Lz = 0·65 to 0·80 mm., lz = 0·35 to 0·50 mm.
        - (i) Median area of fusion extends only along the inner third of each costa ; costae 12–18 ; avicularia very large, broadly oval, prominent, fairly frequent, directed just proximally and outwards from the zooecia they accompany . . 11. ***L. urceolus*** Lang
        - (ii) Median area of fusion extends along the inner two-thirds of each costa ; costae 15–17 ; avicularia rare or absent . 12. ***L. vasculum*** Lang

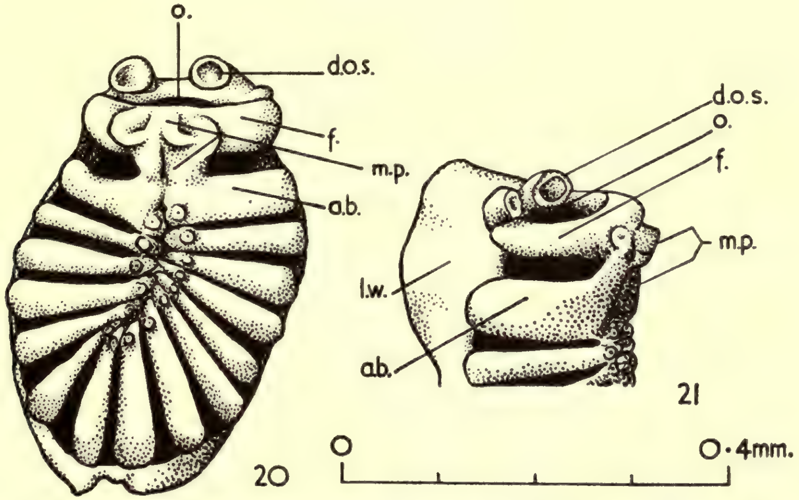
Lepralia pediculus Reuss[1] and *Lagynopora ?prima* (Kühn)[2] are of uncertain systematic position and have therefore been omitted from the above key.

1. *Lagynopora pustulosa*[3] sp. nov.

(Pl. 3, fig. 1 ; Text-figs. 20, 21)

Holotype. D.39419. Small zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Felpham Chalk, Bognor, Sussex.

Paratypes. D.39420–22. Three zoarial fragments encrusting one piece of echinoid test. Senonian, zone of *B. mucronata*. Pit 8 of Rowe, near Nodewell, Freshwater, Isle of Wight.



Figs. 20, 21. *Lagynopora pustulosa* sp. nov., D.39419. Holotype. Front and side view of adult zooecium.

a.b, apertural bar ; *d.o.s*, distal oral spine-bases ; *f*, fusion between median process of apertural bar and proximal oral spines ; *l.w*, lateral wall ; *m.p*, median process of apertural bar ; *o*, orifice.

Diagnosis. *Lagynopora* with zooecia of small size (Lz = 0·50 to 0·53 mm., lz = 0·27 to 0·32 mm.) ; proximal oral shield heavy, large, prominent, very obtusely "Y"-shaped, with a marked median furrow ; frontal shield well arched ; costae 13–16 ; each costa with a distinct small, boss-like pelma at its inner end ; ovicells hyperstomial, globular, small.

Description. *Zoarium* encrusting, unilaminar. *Zooecia* elliptical, closely placed, each with a small, round, *distal communication pore*. *Secondary orifice* distally and laterally rounded, proximal margin straight. *Oral spines* 4, thickened, arranged symmetrically on the distal margin of the orifice. *Proximal oral shield* very prominent, large, very obtusely " Y "-shaped, with a straight distal margin and a marked median furrow, formed by the fusion of the bifurcated median process of the apertural bar with the proximal pair of oral spines. *Frontal shield* well arched. *Costae* 13–16, fairly narrow, tapering inwards and each with a small, boss-like *pelma* very close to its inner end. The pelmata produce two rows of small bosses, one on either side of the mid-line. Distinct, narrow *intercostal spaces* separate the costae. No *lateral costal fusions*. *Median area of fusion* slight. *Apertural bar* wider than the most distal costae, straight, the inner ends of its two component costae curve distally at the mid-line to form the prominent, wide *median process* which bifurcates to form part of the proximal oral shield. *Gymnocyst* concealed by the close placing of the zooecia.

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[1] Lang (1916*a* : 395 ; 1921 : 61) very tentatively placed this species in *Lagynopora*.

[2] *Canupora prima* (Kühn) (1930 : 65) may be a *Lagynopora*, but the available details are insufficient to place it with any certainty.

[3] With reference to the form of the pelmata.

Avicularia apparently absent. *Ovicells* prominent but small, smooth, hyperstomial, globular, of about equal height and width.

MEASUREMENTS. *Zooecia* Lz = 0·50 to 0·53 mm.
lz = 0·27 to 0·32 mm.
hr = 0·09 mm.
lr = 0·15 mm.

[The majority of zooecia in the available specimens are ovicelled or slightly damaged, thus making accurate measurements based on non-ovicelled zooecia difficult.]

REMARKS. This species is clearly distinguished by its boss-like pelmata and its large, prominent and distinctive proximal oral shield.

In the holotype, D.39419, young zooecia are present but not sufficiently well preserved to show whether 4 or 6 oral spines are typically developed at this stage of zoarial growth. The young zooecia apparently do not possess proximal oral shields. The same remarks apply to the young zooecia of the paratypes. In D.39422 some ovicelled zooecia possess prominent, long, proximal oral spines—these seem to be the remains of broken proximal oral shields.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *B. mucronata*.

SPECIMENS. D.39419. Holotype—see above.
D.39420–22. Paratypes—see above.

2. *Lagynopora horsleyensis* Lang

(Pl. 3, figs. 2, 3 ; Text-fig. 22)

1916*a* *Lagynopora horsleyensis* Lang, pp. 395, 396.
1921 *Lagynopora horsleyensis* Lang : Lang, pp. xciii, 57, pl. 2, fig. 3 ; text-fig. 28.
?1958 *Lagynopora horsleyensis* Lang : Didon, pp. 80, 84, text-fig. 2.

HOLOTYPE. D.28908. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*. Pit 264 of Young, Coombs Pit, West Horsley, north-east of Guildford, Surrey.

EMENDED DIAGNOSIS. *Lagynopora* with 14–17 costae, each with 3, occasionally only 2, distinct lateral costal fusions ; avicularia occasional, large, oval, interzooecial, directed distally and obliquely outwards from the zooecia they accompany.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Zooecia* broadly oval, fairly closely placed, with large, oval *distal communication pores*. *Secondary orifice* wider than high, rounded distally with straight sides and a straight proximal margin. *Proximal oral shield* probably formed by the fusion of the lateral oral spines with the median process of the apertural bar ; this structure is usually destroyed by wear. *Oral spines* 4, somewhat thickened, but otherwise unmodified. *Frontal shield* flatly arched. *Costae* 14–17, tapering inwards, each with 3, occasionally only 2, distinct *lateral costal fusions*. Outermost *intercostal spaces* long and slot-like, inner intercostal spaces small and regular. *Median area of fusion* narrow, outwards from the midline the costae are almost horizontal but turn down fairly steeply beyond the outermost lateral costal fusions to meet the gymnocyst. Minute *pelmatidia* are present on the costae at the levels of the lateral costal fusions, and at least one other pelmatidium apparently occurs near the outer end of each costa. *Apertural bar* a little wider than the most distal costae, distally bent at its outer ends and with a *median*

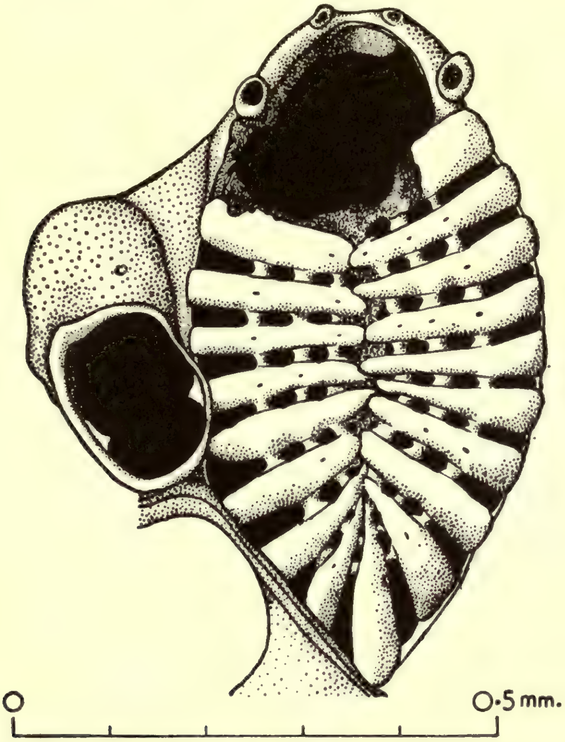


FIG. 22. *Lagynopora horsleyensis* Lang, N.C.M.247.956 (4/2). Adult zooecium with damaged apertural bar, the proximal oral shield worn away. A large interzooecial avicularium with proximal-lateral constrictions is shown to the left of the zooecium.

process. This probably fused with the lateral oral spines to produce a proximal oral shield. *Gymnocyst* apparently smooth, exposed proximally to some frontal shields, but generally obscured by the close placing of the zooecia. *Interzooecial secondary tissue* apparently absent.

Avicularia interzooecial, of one kind, large, oval but somewhat parallel-sided, unpaired, with proximal-lateral constrictions separating a smaller proximal portion from a larger, rounded *rostrum* ; apparently directed distally and obliquely outwards from the zooecia they accompany. *Ovicells* prominent, smooth, hyperstomial, usually longer than wide, tending to be pointed distally.

MEASUREMENTS. *Zooecia* Lz = 0·47 to 0·57 mm.
lz = 0·30 to 0·40 mm.
hr = 0·09 to 0·10 mm.
lr = 0·12 to 0·15 mm.
Avicularia Lz = 0·15 to 0·22 mm.
lz = 0·10 to 0·17 mm.

REMARKS. *Lagynopora horsleyensis* is easily distinguished from other species of the genus by its distinct lateral costal fusions. It is unfortunate that in the available specimens all the proximal oral shields have been destroyed by wear, only the worn median process of the apertural bar and the somewhat lengthened and thickened form of the lateral oral spines suggesting the original presence of this structure. D.40942 extends the upward range of the species into the zone of *G.* [*A.*] *quadrata*.

Lang (1921 : 57) slightly overestimated the dimensions of *L. horsleyensis* and its number of costae. His text-figure 28 and pl. 2, fig. 3, do not indicate the very distinct form of the lateral costal fusions.

Didon (1958) has assigned to this species a poorly preserved specimen from the Santonian of Le Trait, near Rouen, France.

STRATIGRAPHICAL DISTRIBUTION. Senonian, upper part of zone of *M. cor-anguinum* to zone of *G.* [*A.*] *quadrata* and ? Santonian of Le Trait, near Rouen, France.

SPECIMENS. D.28908. Holotype—see above.

D.29899. Incomplete zoarium encrusting a shell fragment. Senonian, zone of *M. cor-anguinum*. Pit in Houndean Bottom, west of Lewes, Sussex.

D.40942. Incomplete zoarium encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 12 of Gaster, Broadwater Pit, north of waterworks pumping station, top of Waterworks Lane, north of Broadwater, near Worthing, Sussex.

D.41069. Small zoarial fragment of six young zooecia encrusting a piece of *Inoceramus* shell. Senonian, high in the zone of *M. cor-anguinum*. Locality and collection as for D.29899.

OTHER MATERIAL

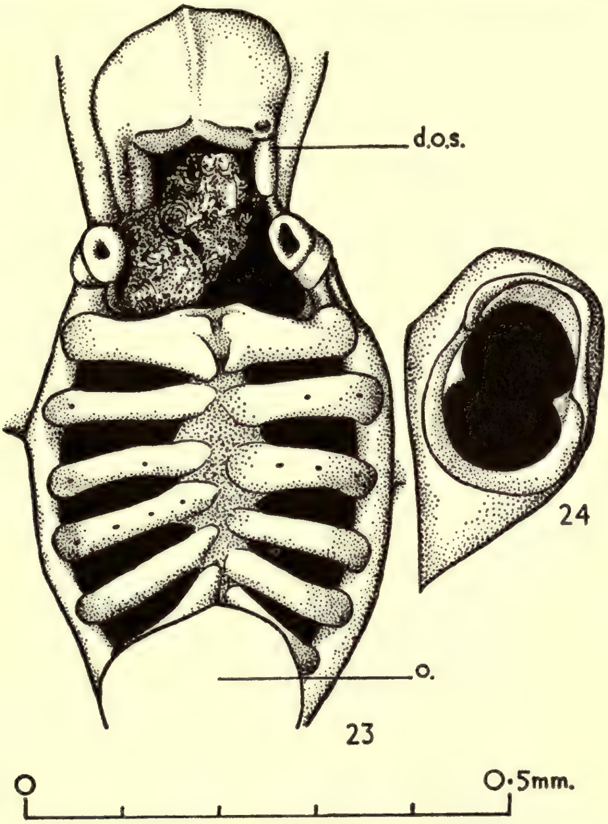
N.C.M.3951. Zoarial fragment with numerous ovicells encrusting the base of a whole test of *Conulus albogalerus*. Senonian, zone of *M. cor-anguinum*. Northfleet, Kent. A. W. Rowe Collection.

3. *Lagynopora praecursor* (Lang) nov. comb

(Pl. 3, fig. 5; Text-figs. 23, 24)

1916*a*	*Prodromopora praecursor* Lang, p. 394.
1921	*Prodromopora praecursor* Lang: Lang, pp. lxiii, xciv, 51, pl. 2, fig. 1; text-fig. 25.
1935	*Prodromopora praecursor* Lang: Bassler, p. 176.
1953	*Prodromopora praecursor* Lang: Bassler, p. G188, text-fig. 142, 8.

HOLOTYPE. D.8351. Zoarial fragment with many damaged ovicelled zooecia and a broken ancestrular area, encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*. Gillingham, north-east of Chatham, Kent. W. Gamble Collection.



FIGS. 23, 24. *Lagynopora praecursor* (Lang), D. 8351. Holotype.

(23) Ovicelled adult zooecium, proximal oral shield worn away; *d.o.s*, distal oral spines; *o*, outline of ovicell of preceding zooecium.

(24) Interzooecial avicularium, of the same zoarium, showing lateral constrictions. The avicularium is figured in the normal orientation to the zooecium—directed distally and obliquely outwards.

EMENDED DIAGNOSIS. *Lagynopora* with small zooecia (Lz = about 0·60 mm., lz = 0·40 to 0·42 mm.); frontal shield well arched; costae 11–13, narrow, separated by wide intercostal spaces; median area of fusion narrow; avicularia frequent, apparently of one kind only, large (Lz = 0·23 mm., lz = 0·15 to 0·20 mm.), oval or almost parallel-sided with proximal-lateral constrictions, directed distally and often obliquely outwards from the zooecia they accompany; ovicells hyperstomial, often with a slight median ridge and small lateral slits.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* oval, fairly closely placed, each with a large, round *distal communication pore*. *Secondary orifice* wider than high, rounded distally and laterally with a straight proximal margin. *Oral spines* 4, arranged symmetrically; the distal pair are smaller than the proximal-lateral pair and may flank the entrance to the ovicell when this is present. The proximal-lateral pair are enlarged; they very probably fused with the median process of the apertural bar to form a *proximal oral shield*. *Frontal shield* well arched, sloping down steeply at the margins to meet the gymnocyst. *Costae* 11–13, narrow, fused only near the mid-line and separated by wide *intercostal spaces*. Some costae retain minute *pelmatidia* along their mid-line. *Apertural bar* well formed, only slightly wider than the most distal costae, with a *median process* which probably fused with the proximal-lateral oral spines to form the proximal oral shield. *Gymnocyst* exposed proximally to most frontal shields and narrowly along their sides. No *interzooecial secondary tissue*.

Avicularia of one kind, very large, frequent, directed distally and often obliquely outwards from the zooecia they accompany. The avicularia are oval or almost parallel-sided with well-marked proximal-lateral constrictions which may be the remains of worn transverse bars. Sometimes the constrictions may be completely removed by wear. *Ovicells* prominent, hyperstomial, globular, smooth, of medium size, often with a slight median ridge and with small *lateral slits*. *Young zooecia* smaller than the adult zooecia and with 6 oral spines. *Ancestrula* apparently with 6 oral spines.

MEASUREMENTS. *Adult zooecia* Lz = about 0·60 mm.
lz = 0·40 to 0·42 mm.
hr = 0·10 to 0·12 mm.
lr = 0·14 to 0·15 mm.
Avicularia Lz = 0·23 mm.
lz = 0·15 to 0·20 mm.
Young zooecia Lz = 0·37 to 0·42 mm.
lz = 0·26 to 0·30 mm.
hr, lr } Not measurable.
Ancestrula Lz = 0·29 mm.
lz = 0·21 mm.
hr, lr } Not measurable.

REMARKS. *Prodromopora praecursor* Lang is placed in *Lagynopora*, as it apparently has a proximal oral shield formed by the fusion of the proximal-lateral oral spines with the median process of the apertural bar. Further, a prominent distal communication pore is present, there are 4 oral spines in the adult zooecia, and large, distally directed oval avicularia are present. All these characters are typical of *Lagynopora*. Unlike most other species of *Lagynopora*, there are only a few widely spaced costae which fuse only along the mid-line of the frontal shield: this distinctive frontal shield is only specifically diagnostic.

Only one specimen, D.8351, is available. Apart from three adult zooecia the zoarium is badly damaged. It is, however, possible, using high-power magnification, to distinguish minute pelmatidia on the costae of these zooecia.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum*.

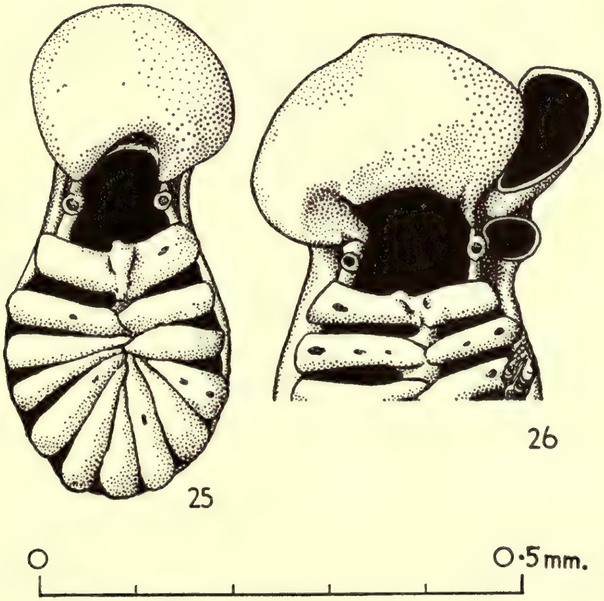
SPECIMEN. D.8351. Holotype—see above.

4. ***Lagynopora saltdeanensis*** Lang

(Pl. 3, fig. 4; Text-figs. 25, 26)

1916*a*	*Lagynopora saltdeanensis* Lang, p. 395.
1921	*Lagynopora saldeanensis* Lang: Lang, pp. xcii, 56, text-fig. 27.
1930	*Lagynopora saltdeanensis* Lang: Gaster, table opp. p. 340.

HOLOTYPE. D.28896. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs between last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.



FIGS. 25, 26. *Lagynopora saltdeanensis* Lang, D.28896. Holotype.

(25) Adult ovicelled zooecium in which the proximal oral shield has been worn away.

(26) Distal half of another adult ovicelled zooecium with two worn interzooecial avicularia.

EMENDED DIAGNOSIS. *Lagynopora* with fairly small zooecia (Lz = 0·43 to 0·45 mm., lz = 0·25 to 0·27 mm.) ; secondary orifice fairly small (hr = 0·08 mm., lr = 0·10 mm.) ; costae, 11–14, with distinct intercostal spaces, but no lateral costal fusions ; avicularia occasional, fairly large, oval ; ovicells hyperstomial.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, closely placed. *Secondary orifice* small, wider than high, rounded distally with straight sides and a straight proximal margin. *Oral spines* apparently 4, not much thickened. *Proximal oral shield* formed by the fusion of the lateral oral spines with the median process of the apertural bar. Nearly all zooecia are worn, retaining only the abraded median process on the apertural bar. *Frontal shield* well arched. *Costae* 11–14, narrow, tapering inwards, united along the mid-line in a narrow *median area of fusion*. Outwards from the median area the costae slope down fairly steeply to meet the gymnocyst. Two or three small *pelmatidia* are visible on the upper surfaces of most costae, but they may be obscured by wear. *Apertural bar* straight with a *median process* which is fused with the proximal-lateral oral spines to produce the proximal oral shield. *Gymnocyst* smooth, fairly widely exposed proximally to each frontal shield, but it may be concealed by the close placing of the zooecia or by the small amounts of *interzooecial secondary tissue* which may occur.

Avicularia occasional, unpaired, fairly large, oval, and of uncertain orientation. *Ovicells* large, smooth, prominent, hyperstomial, globular, of about equal height and width and apparently without *lateral slits*. *Young zooecia* similar to the adult zooecia, but smaller and with fewer costae.

MEASUREMENTS. *Adult zooecia* Lz = 0·43 to 0·45 mm.
lz = 0·25 to 0·37 mm.
hr = 0·08 mm.
lr = 0·10 mm.
Young zooecia Lz = 0·30 to 0·33 mm.
lz = 0·20 to 0·25 mm.
hr = 0·06 mm.
lr = 0·09 mm.
Avicularia Not measurable.

REMARKS. *L. saltdeanensis* is smaller than *L. birlingensis* and possesses fewer costae, and has, apparently, fewer, larger, sporadic avicularia. The only available specimen of *L. saltdeanensis* is the holotype—D.28896. It possesses only a few well-preserved zooecia, at least two of which are representative of a young stage of zoarial growth. It might thus be argued that D.28896 is merely an early growth stage of *L. birlingensis*. The problem can only be settled when new material becomes available.

The form of the proximal oral shield in *L. saltdeanensis* is unknown, but this feature has generic rather than specific diagnostic value and its original presence can be determined with certainty from the form of the worn orifice.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*.

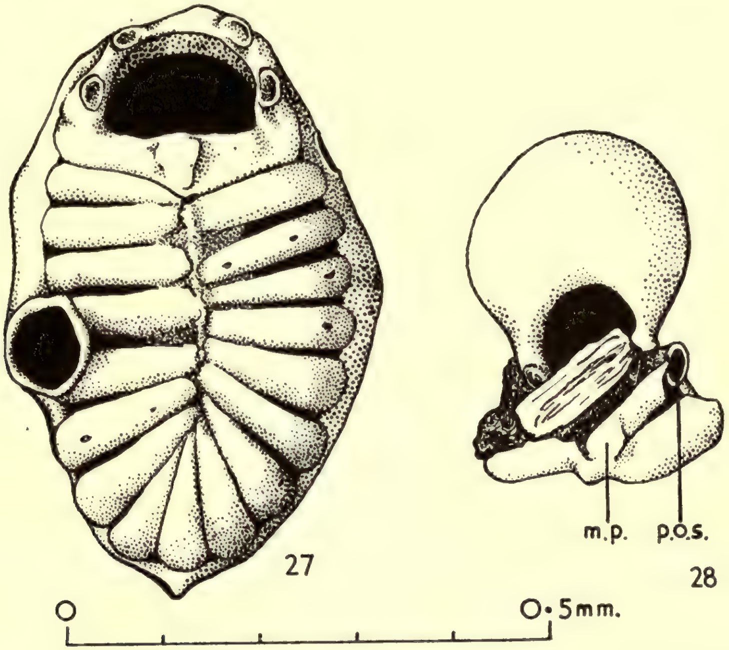
SPECIMEN. D. 28896. Holotype—see above.

5. *Lagynopora birlingensis* Lang

(Pl. 3, fig. 6 ; Text-figs. 27, 28)

1916*a* *Lagynopora birlingensis* Lang, p. 395.
1921 *Lagynopora birlingensis* Lang : Lang, pp. xciv, 55, pl. 2, fig. 2 ; text-fig. 26.
1930 *Lagynopora birlingensis* Lang : Gaster, table opp. p. 340.

HOLOTYPE. D.28254. Incomplete zoarium encrusting a fragment of *Inoceramus* shell. Senonian, zone of *M. cor-anguinum.* Cliffs between Beltout and Birling Gap, west of Beachy Head, Sussex.



FIGS. 27, 28. *Lagynopora birlingensis* Lang, D.28254. Holotype.
(27) Adult zooecium with worn orifice, the proximal oral shield worn away, and worn, oval avicularium.
(28) Ovicell and orifice, partly obscured by matrix, of another adult zooecium—the proximal oral shield is partly preserved ; *m.p*, median process of apertural bar ; *p.o.s*, proximal oral spine.

EMENDED DIAGNOSIS. *Lagynopora* with fairly large zooecia (Lz = 0·50 to 0·60 mm., lz = 0·30 to 0·37 mm.) ; secondary orifice of normal size (hr = 0·10 mm., lr = 0·12 to 0·16 mm.) ; costae numerous (17–18) with distinct intercostal spaces ; no lateral costal fusions ; avicularia interzooecial, oval, fairly abundant ; ovicells hyperstomial, longer than wide.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, fairly closely placed. *Secondary orifice* wider than high, rounded distally and laterally, proximal margin fairly straight. *Oral spines* 4, somewhat thickened but otherwise unmodified, arranged in two pairs on the distal-lateral margins of the orifice. *Proximal oral shield* very obtusely " Y "-shaped, formed by the fusion of the proximal-lateral pair of oral spines with the median process of the apertural bar. *Frontal shield* fairly well arched. *Costae* 17–18, narrow, tapering inwards and separated by distinct, narrow *intercostal spaces* : no *lateral costal fusions* present. The costae are united about the mid-line into a narrow *median area of fusion* in which may be traced the outlines of the inner ends of individual costae. Minute *pelmatidia* are present, possibly three or four on each costa. *Apertural bar* prominent with a *median process* forming part of the proximal oral shield—it is often destroyed by wear leaving a straight apertural bar with a worn median process. *Gymnocyst* exposed proximally to some frontal shields but generally obscured by the small amount of irregular but widespread *interzooecial secondary tissue.*

Avicularia interzooecial, unpaired, numerous, small, rounded to oval, of uncertain orientation. *Ovicells* hyperstomial, smooth, prominent, globular, somewhat longer than wide and without *lateral slits*. *Young zooecia* smaller than the adult zooecia, with fewer (11 or 12) costae, but otherwise similar.

MEASUREMENTS. *Adult zooecia* Lz = 0·50 to 0·60 mm.
lz = 0·30 to 0·37 mm.
hr = 0·10 mm.
lr = 0·12 to 0·16 mm.
Young zooecium Lz = 0·35 mm.
lz = 0·22 mm.
hr, lr } Not measurable.
Avicularia Lz = 0·08 to 0·12 mm.
lz = 0·07 to 0·11 mm.

REMARKS. *Lagynopora birlingensis* may be distinguished by its dimensions, the shape of the orifice which is wider than high, by the form of its proximal oral shield and by its numerous costae and avicularia.

In his description of the species Lang (1921 : 55) described the orifices as normal to cribriline ; however, the marked proximal-lateral constrictions typical of cribriline orifices are not present. He also commented " aviculoecia [avicularia] dimorphic, both kinds fairly numerous, sporadically distributed, with more or less circular apertures, which, even in the larger kind, are decidedly smaller than those [i.e., the orifices] of the orthoecia [zooecia] and, at least in the larger kind, bear spines on the distal rim ". I have been unable to distinguish two kinds of avicularia and have not seen the spines which Lang mentioned. In his figure of the species (1921 : 12, text-fig. 2) Lang showed, at the lower left-hand side, a large round pore and a smaller one proximal to it. These might be avicularia, but as they are very worn this remains uncertain. The only complete proximal oral shield in the specimen is shown much improved in Lang's figure. Although it is more obscured by matrix than is indicated, it is possible to determine that it is much more obtusely " Y"-shaped than Lang has shown. He regarded *L. birlingensis* as a " very primitive form, approaching *Prodromopora* [= *Lagynopora*] in the thinness and distant spacing of the costae." See also remarks on *L. saltdeanensis* (p. 74).

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum*.

SPECIMENS. D.28254. Holotype—see above.

D.41068 Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum* (above the " strong *cor-anguinum* tabular flint band"). Cliffs between Birling Gap and Beltout, west of Eastbourne, Sussex.

6. ***Lagynopora amphora*** Lang

(Pl. 3, fig. 9 ; Text-fig. 29)

1916*a* *Lagynopora amphora* Lang, pp. 395, 396.
1921 *Lagynopora amphora* Lang : Lang, pp. xcii, 59, text-fig. 29.
1930 *Lagynopora amphora* Lang : Gaster, table opp. p. 340.

HOLOTYPE. D.28255. Incomplete zoarium encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Cliffs east of Telscombe Staircase, west of Newhaven, Sussex.

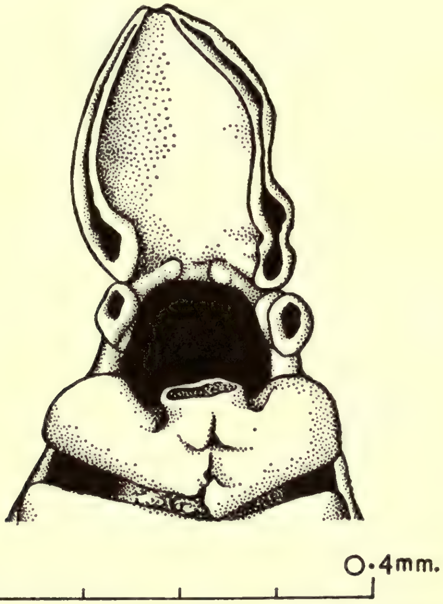


FIG. 29. *Lagynopora amphora* Lang, D.28255. Holotype. Orifice and broken ovicell of adult zooecium. The enlarged proximal oral spines fused originally with the prominent, broken median process of apertural bar.

EMENDED DIAGNOSIS. *Lagynopora* with large zooecia (Lz = 0·64 to 0·75 mm., lz = 0·37 to 0·50 mm.) ; frontal shield often with a distinct median ridge ; costae 13–17 with distinct intercostal spaces ; avicularia interzooecial, small, oval, occasional ; ovicell hyperstomial, slightly pointed distally, slightly longer than wide.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* very closely placed, broadly oval, each with a large, oval distal, and a smaller, oval *lateral communication pore*. *Secondary orifice* wider than high, distally and laterally rounded with a straight proximal margin. *Oral spines* 4, slightly enlarged, arranged symmetrically on the distal and lateral margins of the orifice. *Proximal oral shield* developed, but form unknown, all the oral shields in the available specimens having been destroyed by wear. *Frontal shield* evenly arched, often with a distinct median ridge. *Costae* 13–17, tapering slightly inwards, separated by narrow but distinct *intercostal spaces*. No *lateral costal fusions*. Each costa possesses a series of minute *pelmatidia* on its upper surface. *Median area of fusion* slight, often consisting of the median ridge only, or extending only slightly on either side of it. The outline of the inner extremity of each costa is visible in the median area of fusion. *Apertural bar* wider than the most distal costae, somewhat triangular, with distally curved ends, and with a prominent, fairly wide *median process* which almost certainly fuses, when complete, with the proximal-lateral pair of oral spines to form a proximal oral shield. *Gymnocyst* not exposed, owing to the very close placing of the zooecia. No *interzooecial secondary tissue*.

Avicularia interzooecial, occasional, small, with oval apertures. *Ovicells* hyperstomial, prominent, smooth, globular, longer than wide, sometimes tending to be slightly pointed distally. *Young zooecia* generally resemble the adult zooecia, but are smaller and have 6 oral spines, and slightly fewer (11–14) costae.

MEASUREMENTS. *Adult zooecia* Lz = 0·64 to 0·75 mm.
lz = 0·37 to 0·50 mm.
hr = 0·12 to 0·13 mm.
lr = 0·15 to 0·16 mm.
Young zooecia Lz = 0·40 to 0·47 mm.
lz = 0·30 to 0·35 mm.
hr = 0·11 to 0·12 mm.
lr = 0·13 mm.
Avicularia Not measurable.

REMARKS. *Lagynopora amphora* is distinguished from other species of the genus particularly by the characters of its frontal shield, which, in contrast to that of *L. ampulla*, is evenly arched and unconsolidated. The median ridge is especially distinctive.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*, and lower part of zone of *B. mucronata* (not yet recorded from the zone of *G.* [*A.*] *quadrata*).

SPECIMENS. D.28255. Holotype—see above.

D.40943. Incomplete zoarial fragment with young and adult zooecia, some ovicelled, encrusting a piece of echinoid test. Horizon, locality and collection as for the holotype.

OTHER MATERIAL

N.C.M.76.937(32), 76.937(33). Two zoarial fragments encrusting one piece of echinoid test. Senonian, lower part of zone of *B. mucronata*, Wells, Norfolk. R. M. Brydone Collection.

7. *Lagynopora ampulla* Lang

(Pl. 3, figs. 7, 8; Text-fig. 30)

1916*a*	*Lagynopora ampulla* Lang, pp. 395, 396.
1921	*Lagynopora ampulla* Lang : Lang, pp. xcii, 60, text-fig. 31.
1930	*Lagynopora ampulla* Lang : Gaster, table opp. p. 340.

HOLOTYPE. D.28256. Specimen in five fragments. Incomplete zoarium encrusting a cheilostome polyzoan. Senonian, zone of *G.* [*A.*] *quadrata*. East side of Old Nore Point, west of Newhaven, Sussex.

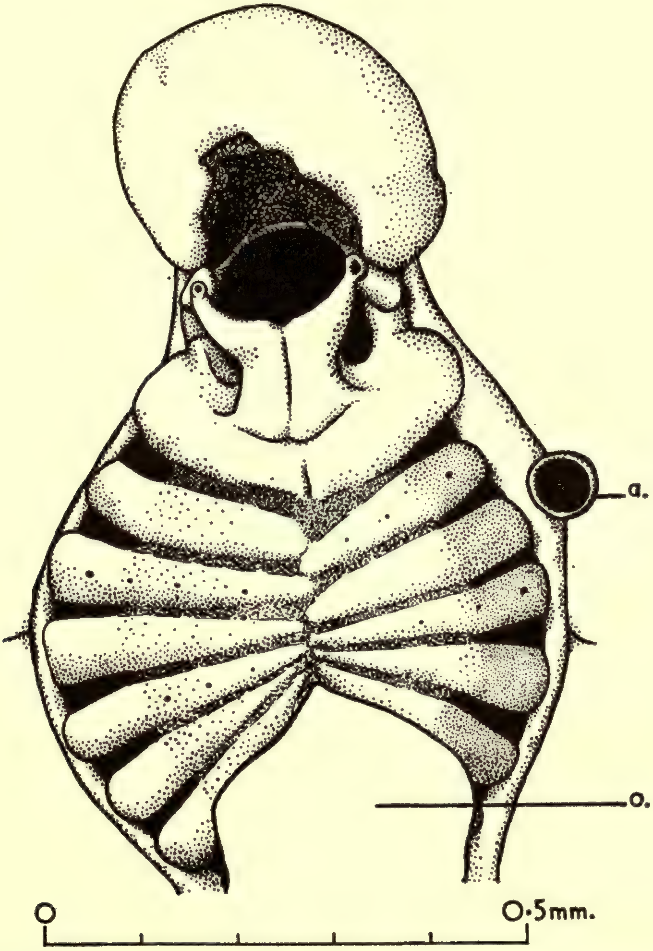


FIG. 30. *Lagynopora ampulla* Lang, D.28256. Holotype. Adult ovicelled zooecium with small, round, worn avicularium (*a*). The ovicell is slightly damaged proximally; the proximal oral shield is well preserved showing the slender fusions with lengthened proximal oral spines and wide median process of apertural bar. *o*, outline of the ovicell of the preceding zooecium.

EMENDED DIAGNOSIS. *Lagynopora* with large zooecia (Lz = 0·62 to 0·75 mm., lz = 0·35 to 0·50 mm.); proximal oral shield obtusely "Y"-shaped, prominent, flat and wide in front with a distinct median furrow, and slender fusions with the proximal-lateral oral spines; costae 12–14, closely placed, no lateral costal fusions.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, closely placed, with large, oval *distal communication pores* and smaller *lateral communication pores*. *Secondary orifice* wider than high, distally rounded with straight sides and a straight proximal margin, the sides of the orifice may converge slightly proximally. The form of the secondary orifice is often obscured by the well-developed proximal oral shield or by ovicells. *Oral spines* 4, slightly lengthened, somewhat thickened, arranged symmetrically on the distal rim of the orifice. *Proximal oral shield* very prominent, obtusely "Y"-shaped, flat and wide in front, composed of the bifurcated, enlarged median process of the apertural bar which fuses, on either side, with the proximal-lateral oral spines. *Frontal shield* very flatly arched, well consolidated. *Costae* 12–14 (often 13). Each costa is fairly flat and tapered inwards. Adjacent costae are in contact and horizontal for most of their length. At their outer ends they bend down steeply to meet the gymnocyst and are separated by short, narrow *intercostal spaces*. Although the costae are in contact with one another, their outlines remain distinct, even in the median area. *Median area of fusion* extremely wide. Minute *pelmatidia* are visible on the upper surfaces of some costae. *Apertural bar* wider than the most distal costae, straight, or slightly curved distally at either end, with a strong *median process* which bifurcates and fuses with the proximal-lateral oral spines to produce the proximal oral shield. *Gymnocyst* apparently smooth, but little exposed owing to the close placing of the zooecia. No *interzooecial secondary tissue*.

Avicularia very occasional, small, circular, interzooecial. *Ovicells* hyperstomial, prominent, smooth, globular, of about equal height and width. The entrance to the ovicell may be prominently flanked by a pair of oral spines. *Young zooecia* similar to the adult zooecia, but smaller and with 5 oral spines, and generally fewer (10–12) costae.

MEASUREMENTS. *Adult zooecia* Lz = 0·62 to 0·75 mm.
lz = 0·35 to 0·50 mm.
hr = 0·14 to 0·15 mm.
lr = 0·15 to 0·17 mm.
Young zooecia Lz = 0·40 to 0·47 mm.
lz = 0·25 to 0·32 mm.
hr = 0·08 to 0·10 mm.
lr = 0·09 to 0·14 mm.
Avicularia Lz = 0·04 mm.
lz = 0·04 mm.

REMARKS. *L. ampulla* is distinguished from other species of *Lagynopora* by its well consolidated frontal shield, short intercostal spaces, and particularly by its proximal oral shield. Lang (1921 : 60) overestimated the zooecial dimensions of *L. ampulla*.

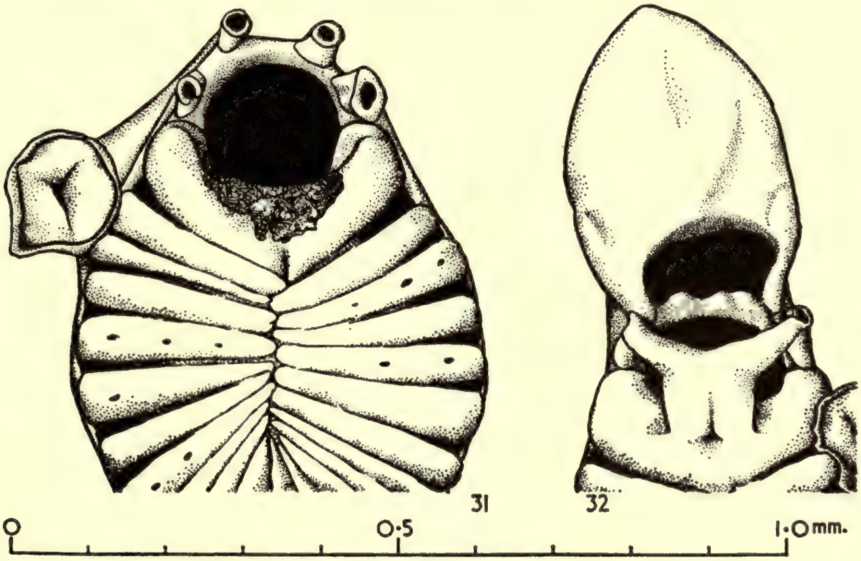
STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *G.* [*A.*] *quadrata*.
SPECIMEN. D.28256. Holotype—see above.

8. *Lagynopora furcifera* (Brydone)

(Pl. 4, figs. 1, 2; Text-figs. 31, 32)

1910 *Cribrilina furcifera* Brydone, pp. 391, 392, 482 [*partim*—pl. 30, fig. 7 only, *non* fig. 6 (= *Lagynopora vasculum*), *non* fig. 8 (= *L. ollula*)].
1916*a* *Lagynopora* [*Cribrilina*] *furcifera* (Brydone): Lang, p. 395 [*partim*—that referring to Brydone, 1910, pl. 30, fig. 7 only].
1917 *Cribrilina furcifera* Brydone: Brydone, p. 492.
1921 *Lagynopora furcifera* (Brydone) Lang, pp. xci, 67.
?1930 *Lagynopora furcifera* (Brydone): Voigt, pp. 495, 542, 560, pl. 26, fig. 10.
?1949 *Lagynopora* aff. *furcifera* (Brydone): Voigt, pp. 36, 43, 44, pl. 11, fig. 1.

LECTOTYPE. (Chosen by Lang, 1921 : 67.) S.M., B.36165. An extensive, well-preserved zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Bramford, near Ipswich, Suffolk. R. M. Brydone Collection.



FIGS. 31, 32. *Lagynopora furcifera* (Brydone), S.M., B.36165. Lectotype.
(31) Adult zooecium and worn avicularium, the proximal oral shield destroyed.
(32) Ovicell and orifice of another adult zooecium with complete proximal oral shield and part of an avicularium.

EMENDED DIAGNOSIS. *Lagynopora* with very large zooecia (Lz = 0·75 to 0·85 mm., lz = 0·50 to 0·56 mm.); proximal oral shield very prominent, very widely " Y "-shaped, composed of a wide median process which rises from the apertural bar, bifurcates, and fuses with the proximal-lateral pair of oral spines; frontal shield well arched; costae very numerous, 20–23, distinct, separated by intercostal spaces for at least half their length ; median area of fusion wide ; avicularia interzooecial, fairly frequent, oval.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, closely placed, each with a large, oval *distal communication pore* and one or two, somewhat smaller, oval *lateral communication pores*. *Secondary orifice* wider than high, rounded distally and laterally with a straight proximal margin. *Oral spines* 4, slightly enlarged, symmetrically arranged round the orifice. *Proximal oral shield* prominent, formed by the fusion of the proximal-lateral pair of oral spines with the wide, flat median process of the apertural bar. *Frontal shield* slightly flattened in the median area but otherwise well arched. *Costae* 20–23, narrow, well defined, separated at their outer ends, and for about half their length, by distinct *intercostal spaces* ; the outlines of their inner ends may be traced across the wide *median area of fusion*. No *lateral costal fusions*. Minute *pelmatidia* are visible on the upper surfaces of unworn costae. *Apertural bar* wide, somewhat swollen, triangular, the apex of the triangle pointing proximally. The outer ends of the apertural bar are slightly bent proximally to the frontal shield, but generally obscured by the close placing of the zooecia, or by avicularia. *Interzooecial secondary tissue* absent.

Avicularia interzooecial, frequent, fairly large, oval. [In the lectotype all the avicularia are worn.] *Ovicells* hyperstomial, frequent, smooth, prominent, globular, some may be slightly pointed distally with a slight median ridge. The proximal-lateral margins of the ovicells normally incorporate the distal pair of oral spines. *Young zooecia* smaller than the adult zooecia but otherwise similar, except that some of the very young zooecia may possess 5 or 6 oral spines, and the orifice tends to be of equal height and width.

MEASUREMENTS. *Adult zooecia* Lz = 0·75 to 0·85 mm.
lz = 0·50 to 0·56 mm.
hr = 0·15 to 0·16 mm.
lr = 0·18 to 0·20 mm.
Young zooecia Lz = 0·57 to 0·63 mm.
lz = 0·40 to 0·52 mm.
hr = 0·15 mm.
lr = 0·15 mm.
Avicularia Lz = About 0·20 mm.
lz = About 0·13 mm.

REMARKS. Brydone figured three specimens with his original description of *Cribrilina furcifera*, 1910, pl. 30, figs. 6–8). Lang (1916*a* : 395) placed these three specimens in a single species of *Lagynopora*. Subsequently (1921) he suggested that the material figured by Brydone as *Cribrilina furcifera* belonged to three separate species of *Lagynopora* (that shown in fig. 6 being *L. vasculum*, that in fig. 7—*L. furcifera*, and that in fig. 8—*L. ollula*).

Having examined Brydone's figured specimens, I agree that they are three separate species of *Lagynopora*. I have accordingly extended the brief diagnoses given by Lang [these were based solely on Brydone's somewhat inadequate figures] and have added full descriptions and measurements.

Lagynopora furcifera (Brydone) possesses more costae than *L. vasculum* or *L. ollula*, and is larger. The degree of consolidation of the arched frontal shield and the avicularia also further distinguish *Lagynopora furcifera* from other species of the genus.

Voigt (1930 : 495, pl. 26, fig. 10) assigned to the species a specimen from the " Quadraten-oder Mukronatensenon " of Misburg. Both the description, in which he stated only that there are about 20 costae and that Lz = 0·70 mm., and the figure, which is quite indistinct, are inadequate to place the material with any certainty. More recently (Voigt, 1949 : 36, pl. 11, fig. 1) has described and figured, as " *Lagynopora* aff. *furcifera* (Brydone) ", another specimen from the " Quadratenkreide " of Lägerdorf, Holstein. It is slightly larger than the lectotype, with slightly fewer costae and with 7 oral spines in the youngest zooecia.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *G.* [*A.*] *quadrata* of England and Germany.

MATERIAL. S.M., B.36165. Lectotype—see above.

9. ***Lagynopora ollula*** Lang

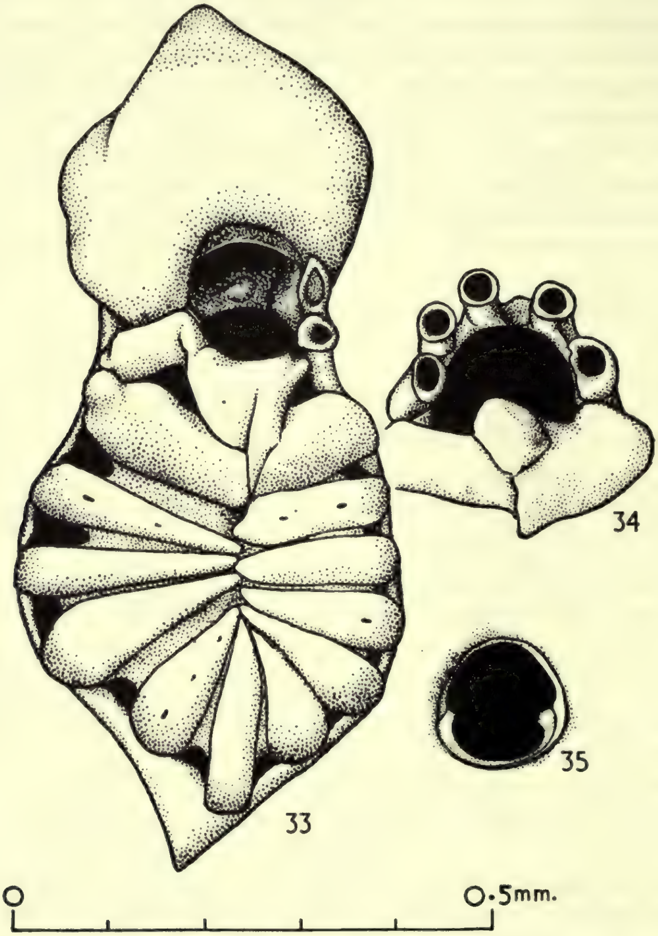
(Pl. 4, fig. 3 ; Text-figs. 33–35)

1910 *Cribrilina furcifera* Brydone, p. 391 [*partim*—pl. 30, fig. 8 only].
1916*a* *Lagynopora furcifera* (Brydone) : Lang, p. 395 [*partim*—that referring to Brydone, 1910, pl. 30, fig. 8 only].
1921 *Lagynopora ollula* Lang, pp. xciv, 60.
1930 *non Lagynopora furcifera* (Brydone) : Voigt, pp. 495, 542, 560, pl. 26, fig. 10.
1949 *non Lagynopora* aff. *furcifera* (Brydone) : Voigt, pp. 36, 43, 44, pl. 11, fig. 1.

LECTOTYPE. (Chosen by Lang, 1921 : 60.) S.M., B.36166. The specimen figured by Brydone (1910, pl. 30, fig. 8). Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites*, subzone of *Uintacrinus*. Kingsgate, Kent. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Lagynopora* with large zooecia (Lz = 0·58 to 0·67 mm., lz = 0·40 to 0·51 mm.) ; orifice of constant size (hr = 0·12 mm., lr = 0·15 mm.) ; proximal oral shield very prominent, obtusely " Y "-shaped, the flat, wide median process standing out almost at right angles to the plane of the apertural bar ; frontal shield well consolidated ; costae 9–11, broad, closely placed, fused to neighbouring costae throughout most of their length ; avicularia interzooecial, unpaired, large, prominent, oval, with proximal-lateral constrictions.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* closely placed, very broadly oval, each with a very large, oval *distal communication pore* and several smaller, oval *lateral communication pores*. *Secondary orifice* wider than high, of constant size, distally rounded with straight sides and a straight proximal margin. The form of the orifice may be obscured by the proximal oral shield or by ovicells. *Oral spines* 4 or 5, arranged symmetrically round the orifice. The proximal-lateral pair of oral spines is often larger than the distal pair, all are slightly secondarily thickened. *Proximal oral shield* very prominent, obtusely " Y "-shaped, formed by the flat, wide median process of the apertural bar which bifurcates and fuses with the lateral pair of oral spines. *Frontal shield* wide, flat, except at the margins where the costae descend steeply to meet the gymnocyst. *Costae* 9–11, distinct, wide, rounded, tapering inwards. Each costa is completely fused to its neighbouring costae for most of its length, but the outline of each costa is clearly visible up to the mid-line of the frontal shield. Only at their outer ends are the costae clearly separate, and the frontal shield is well consolidated and the *median area of fusion* extremely wide. Minute *pelmatidia* are visible on the upper surfaces of unworn costae. *Apertural bar* straight, except for a distal curve at either end, swollen, wider than the most distal costae. A strong, flat, wide *median process* rises almost



FIGS. 33–35. *Lagynopora ollula* Lang, S.M., B.36166. Lectotype.

(33) Adult ovicelled zooecium ; the proximal oral shield is broken on one side.

(34) Orifice of another adult zooecium with a fifth distal-median oral spine-base ; the proximal oral shield broken.

(35) Avicularium with proximal-lateral constrictions.

perpendicularly from the centre of the apertural bar and forms part of the proximal oral shield. *Gymnocyst* smooth, but seldom exposed owing to the close placing of the zooecia; usually visible round the interzooecial avicularia. No *interzooecial secondary tissue.*

Avicularia interzooecial, unpaired, large, round or oval, probably with a *transverse bar,* now broken, and represented by proximal-lateral constrictions, originally dividing a smaller semicircular proximal portion from a larger, transversely oval *rostrum.* Apparently the avicularia are variously directed; some are definitely distally directed obliquely away from the zooecia they accompany, others may be directed proximally and obliquely towards the zooecia they accompany.

Ovicells hyperstomial, very prominent, smooth, globular, as wide as high. The proximal-lateral margin of the ovicell may incorporate or obscure the distal-lateral pair of oral spines. Some ovicells tend to be slightly pointed distally.

Young zooecia smaller than the adult zooecia. Orifice of less constant size than in the adult stages. Oral spines 6 or 7. Proximal oral shield probably developed. Frontal shield more arched than in the adult. Costae more numerous, 10–12, but, as in the adult stages, fused for most of their length. Apertural bar wide, straight.

Ancestrula [of lectotype]. Only the orifice is visible; it is wider than high, and there are 8 closely spaced, symmetrically arranged oral spines.

Measurements. *Adult zooecia* Lz = 0·58 to 0·67 mm.
lz = 0·40 to 0·51 mm.
hr = 0·12 mm.
lr = 0·15 mm.
Avicularia Lz = 0·12 to 0·14 mm.
lz = 0·19 to 0·15 mm.
Young zooecia Lz = 0·40 to 0·43 mm.
lz = 0·23 to 0·26 mm.
hr = 0·07 to 0·10 mm.
lr = 0·10 to 0·11 mm.
Ancestrula $\left.\begin{array}{l}\text{Lz}\\ \text{lz}\end{array}\right\}$ Not measurable.
hr = 0·07 mm.
lr = 0·10 mm.

Remarks. *Lagynopora ollula* (Brydone) is clearly distinguished from other species of the genus by its much consolidated, wide frontal shield, its relatively few costae, the constant size of its orifice, and particularly by the characters of its avicularia.

In the lectotype, S.M., B.36166, where ovicells have been preserved they apparently afforded some protection for the proximal oral shield, for this is most complete in the ovicelled zooecia. In non-ovicelled zooecia, although the proximal oral shield is very prominent, it is frequently destroyed by wear so that the apertural bar appears as a straight, featureless structure with no trace of the very strong median process present in complete individuals. Very slight wear of the surfaces of the costae in this well-preserved specimen has been sufficient to obscure most of the minute pelmatidia which may now be seen only occasionally on the upper surfaces of some costae.

The lectotype zoarium, although small, is almost complete, for it possesses the ancestrula and its surrounding young zooecia, ovicelled adult zooecia, and, in one place, a small zooecium possibly close to part of the growing edge of the zoarium.

Fewer oral spines are developed in the adult than in the young stages, and the ancestrula possesses the largest number of oral spines, 8. This reduction in the number of oral spines during growth is apparently accompanied by a slight reduction in the number of costae.

Lang (1921 : 60) has suggested that *L. ollula*, apart from its well-consolidated frontal shield, shows " primitive characters ".

Mr. A. G. Brighton has kindly informed me that Brydone (*in litt.* 23rd June, 1938) stated that the lectotype came from the " *Uintacrinus* Band " of Kingsgate, Kent.

See also remarks under *L. furcifera* (Brydone), p. 82.

Stratigraphical distribution. Senonian, zone of *Marsupites*, subzone of *Uintacrinus*.

Material. S.M., B.36166. Lectotype—see above.

10. ***Lagynopora lagena*** Lang

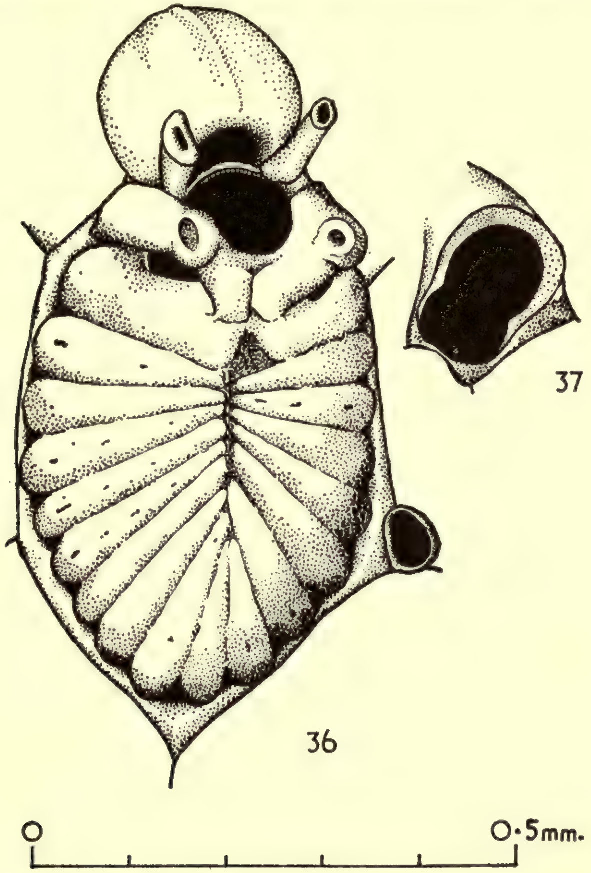
(Pl. 4, figs. 4–6 ; Text-figs. 36, 37)

1893	*Cribrilina nitidiformis* Vine, pp. 316, 336 [*nomen nudum*—*vide* Lang, 1921 : 62].
1904	*Cribrilina nitidiformis* Vine : Jukes-Browne, p. 490 [*vide* Lang, 1921 : 62].
1916*a*	*Cribrilina nitidiformis* Vine : Lang, p. 410 [*vide* Lang, 1921 : 62].
1916*a*	*Lagynopora lagena* Lang, p. 395.
1921	*Lagynopora lagena* Lang : Lang, pp. lxi, xciv, 62, pl. 2, fig. 4 ; text-fig. 30.
?1930	*Lagynopora* aff. *lagena* Lang : Voigt, pp. 495, 542, 560, pl. 26, fig. 9.
1935	*Lagynopora lagena* Lang : Bassler, p. 135.
1953	*Lagynopora lagena* Lang : Bassler, p. G188, text-fig. 142, 9.

Holotype. D.4042. Zoarial fragment encrusting a piece of echinoid test. Senonian, either zone of *M. cortestudinarium* or zone of *M. cor-anguinum*. Chatham, Kent. W. Gamble Collection.

Emended diagnosis. *Lagynopora* with zooecia of medium size (Lz = 0·48 to 0·68 mm., lz = 0·35 to 0·46 mm.) ; proximal oral shield more acutely " Y "-shaped than in other species of *Lagynopora*, formed by a fairly narrow median process of the apertural bar which fuses with large, robust proximal-lateral oral spines ; frontal shield evenly arched ; costae 13–20 (often 15–19), juxtaposed but delimited for their whole length by distinct furrows and united only in the narrow median area of fusion which may form a slight ridge ; avicularia frequent, apparently of two sizes, interzooecial, oval with proximal-lateral constrictions ; ovicells hyperstomial, often with a slight median ridge, occasionally with small lateral slits.

Description. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, fairly closely placed, each with an oval *distal communication pore. Secondary orifice* wider than high, rounded distally and laterally with a straight proximal margin. *Oral spines* 4, symmetrically arranged round the orifice, the proximal-lateral pair slightly larger than the distal pair. *Proximal oral shield* prominent, more acutely "Y"-shaped than in other species of *Lagynopora*, formed by the narrow median process of the apertural bar which fuses with the proximal pair of robust oral spines. *Frontal shield* well arched, with a slight, often ridge-like, narrow *median area of fusion*. *Costae* 13–20, variable in number but often 15–19, narrow, juxtaposed but defined along their whole length by distinct furrows and properly fused only along the mid-line of the frontal shield. No *lateral costal fusions*. Minute *pelmatidia* are visible on the upper surfaces of some well-preserved costae. *Apertural bar* wider than the most distal costae, straight, with a slight distal bend at either end, and with



FIGS. 36, 37. *Lagynopora lagena* Lang.

(36) D.4042. Holotype. Adult ovicelled zooecium with complete proximal oral shield and small oral, worn avicularium of type *b*. The distal oral spines are unusually long.

(37) D.2633. Paratype. Large interzooecial avicularium of type *a*, shown in relation to Fig. 36 in the usual orientation for the species—directed distally and obliquely outwards from the zooecium.

a narrow *median process* which forms part of the proximal oral shield. *Gymnocyst* smooth, only slightly exposed proximally to some frontal shields or more extensively round some avicularia, but generally concealed by the close placing of the zooecia. No *interzooecial secondary tissue*.

Avicularia of one kind, but, in some zoaria, of two sizes, interzooecial, oval with proximal-lateral constrictions which are, apparently, the broken ends of straight *transverse bars*. Where avicularia of both sizes are developed, the larger type (*a*) occurs near the orifice and is directed distally and obliquely outwards from the zooecium it accompanies. The small type (*b*) occurs less frequently and always distal to the orifice or distal to the ovicell when this is present, and is distally directed. In zoaria with both types the avicularia occur frequently, but they are less numerous in zoaria with only the larger form. Where only the larger form of avicularium occurs it may also be placed distally to the orifice. Occasionally avicularia are rare or even absent in a zoarium. No example has been seen in which only the smaller type of avicularium occurs. *Ovicells* hyperstomial, small but prominent, smooth, globular, wider than high and often with a median ridge. Occasional ovicells may have small *lateral slits*. *Young zooecia* resemble the adult zooecia, but are smaller and may have from 4 to 6 oral spines and fewer costae. Often the youngest zooecia have the most oral spines. *Ancestrulae* lack the proximal oral shield which occurs throughout young and adult zooecia. Some ancestrulae possess 6 oral spines, that of D.11280, however, has only 4.

MEASUREMENTS. *Adult zooecia* Lz = 0·48 to 0·68 mm.
lz = 0·35 to 0·46 mm.
hr = 0·10 to 0·13 mm.
lr = 0·13 to 0·18 mm.
Avicularia :
Type *a* Lz = 0·18 to 0·20 mm.
lz = 0·15 to 0·17 mm.
Type *b* Lz = 0·10 to 0·11 mm.
lz = 0·07 to 0·08 mm.
Young zooecia Lz = 0·40 to 0·45 mm.
lz = 0·26 to 0·33 mm.
hr = 0·07 mm.
lr = 0·11 mm.
Ancestrula (of D.11280) Lz = 0.30 mm.
lz = 0·23 mm.
hr = 0·07 mm.
lr = 0·10 mm.

REMARKS. *Lagynopora lagena*, the type species, was regarded by Lang (1921 : 63) as " the lowest term in a series " which, he suggested, exhibits an increasing consolidation of the frontal shield and a gradual loss of avicularia, first of the smaller kind [type (*b*) in *L. lagena*] and finally of the larger kind also. Certainly *L. lagena* is the only species of *Lagynopora* which possesses more than one size of avicularium, and it also exhibits, though not necessarily in a single zoarium, the widest range in number of costae. Like other species, it undergoes, in the early stages of zoarial growth, a rapid reduction in the number of oral spines.

L. lagena is distinguished by its large number of costae, its well-arched frontal shield and narrow, ridge-like median area of fusion, and by its avicularia and small ovicells.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *M. cortestudinarium* and *M. cor-anguinum* in England. ?Upper part of zone of *G.* [*A.*] *quadrata* in Germany.

SPECIMENS. D.4042. Holotype—see above.

D.4027–28. Two paratype zoarial fragments, the former encrusting an erect cheilostome polyzoan, the latter with only one complete zooecium and now unattached. Horizon, locality and collection as for the holotype.

D.4046. Paratype. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for the holotype.

D.4238. Paratype. Zoarial fragment encrusting a piece of *Inoceramus* shell. Horizon, locality and collection as for the holotype.

D.4969–70, D.4974–76, D.27978–79. Seven paratypes. Zoarial fragments encrusting pieces of echinoid tests. Horizon, locality and collection as for the holotype.

D.2633. Paratype. Zoarial fragment encrusting part of an erect cheilostome polyzoan. Labelled " Syntype of *Cribrilina nitidiformis* Vine 1893 ". Horizon and locality as for the holotype. G. R. Vine Collection.

D.2640. Paratype. Zoarial fragment encrusting a piece of *Inoceramus* shell. Labelled " Syntype of *Cribrilina nitidiformis* Vine 1893 ". Horizon and locality as for the holotype. G. R. Vine Collection.

D.11280. Paratype. Zoarial fragment encrusting a piece of test of *Micraster precursor* Rowe. Senonian, top of zone of *M. cortestudinarium* or base of zone of *M. cor-anguinum.* Chatham, Kent. W. Gamble Collection.

D.21209. Paratype. Zoarial fragment with young zooecia possessing six oral spines encrusting a small fragment of echinoid test. Senonian, zone of *M. cor-anguinum.* Woburn Green, south-west of Beaconsfield, Buckinghamshire. L. Treacher Collection.

D.24236–38. Three paratypes. Zoarial fragments encrusting pieces of echinoid test. Senonian, high in zone of *M. cortestudinarium.* Luton, south-east of Chatham, Kent. W. Gamble Collection.

D.24385. Paratype. Extensive zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum.* Locality and collection as for D.24236–38.

D.24519–20. Two paratypes. Zoarial fragments encrusting pieces of echinoid test, the former with small avicularia of type (*b*). Senonian, zone of *M. cor-anguinum.* Gillingham, north-east of Chatham, Kent. W. Gamble Collection.

D.24525. Paratype. Zoarial fragment with numerous avicularia of type (*a*) and with a regenerated and reversed zooecium, encrusting a piece of echinoid test. Horizon, locality and collection as for D.24519–20.

D.8135, D.24136, D.24541. Three paratypes. Zoarial fragments; D.8135 encrusting an erect polyzoan, the remainder encrusting pieces of echinoid test. Horizon, locality and collection as for D.24519–20.

D.24539, D.24592. Two paratypes. Zoarial fragments, the former encrusting an erect cyclostome polyzoan, the latter encrusting an erect cheilostome polyzoan. Horizon, locality and collection as for D.24519–20.

D.27039–40. Two paratypes. Zoarial fragments encrusting the dorsal surface of pieces of unattached cheilostome polyzoan zoaria. Senonian, zone of *M. cortestudinarium*. Lower Pit, Slines Oak, Worms Heath, Warlingham, Surrey. F. Möckler Collection.

D.27854–56. Three paratypes Zoarial fragments encrusting pieces of echinoid tests. Senonian, zone of *M. cortestudinarium* (upper part). Locality and collection as for D.24519–20.

D.29102. Paratype. Zoarial fragment encrusting three pieces of echinoid test. Senonian, zone of *M. cor-anguinum*. Keston, Kent (south-east of Croydon, Surrey). R. Jones Collection.

11. ***Lagynopora urceolus*** Lang

(Pl. 4, fig. 7; Pl. 5, fig. 1; Text-figs. 38, 39)

1916*a* *Lagynopora urceolus* Lang, pp. 395, 396.
1921 *Lagynopora urceolus* Lang: Lang, p. 65, pl. 2, fig. 5; text-fig. 32.
1930 *Lagynopora urceolus* Lang: Gaster, table opp. p. 340.

HOLOTYPE. D.28889. Zoarial fragment with ancestrula and ovicelled adult zooecia encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs between last groyne east of Rottingdean Gap and Saltdean, Sussex.

EMENDED DIAGNOSIS. *Lagynopora* with zooecia of large size (Lz = 0·65 to 0·78 mm., lz = 0·35 to 0·50 mm.); orifice just wider than high; frontal shield well arched; costae 12–18, closely placed; no marked intercostal spaces; avicularia larger than the orifice, interzooecial, fairly frequent, directed just proximally and outwards from the zooecia they accompany; ovicells large.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, each with a large, circular *distal communication pore* and one or more smaller, oval *lateral communication pores*. *Secondary orifice* just wider than high, rounded distally and laterally with a straight proximal margin. *Oral spines* 4, occurring in two distinct pairs, the proximal pair larger. *Proximal oral shield* obtusely " Y "-shaped, formed by the fusion of the proximal oral spines with the bifurcated median process of the apertural bar. *Frontal shield* well arched, but flattened in the median area. *Costae* 12–18, closely placed, separated by furrows rather than definite *intercostal spaces*, but with their outlines distinct. *Median area of fusion* not very wide, extending along the inner half of the costae at the maximum. The mid-line of the frontal shield may be marked by a slight, irregular ridge. No *lateral costal fusions*. Minute *pelmatidia* are visible on the upper surfaces of well-preserved costae. *Apertural bar* widely triangular, the apex pointing proximally, with a median ridge and a prominent *median process* which forms part of the proximal oral shield. *Gymnocyst* smooth, almost completely concealed by the close placing of the zooecia and by ovicells and avicularia. No *interzooecial secondary tissue.*

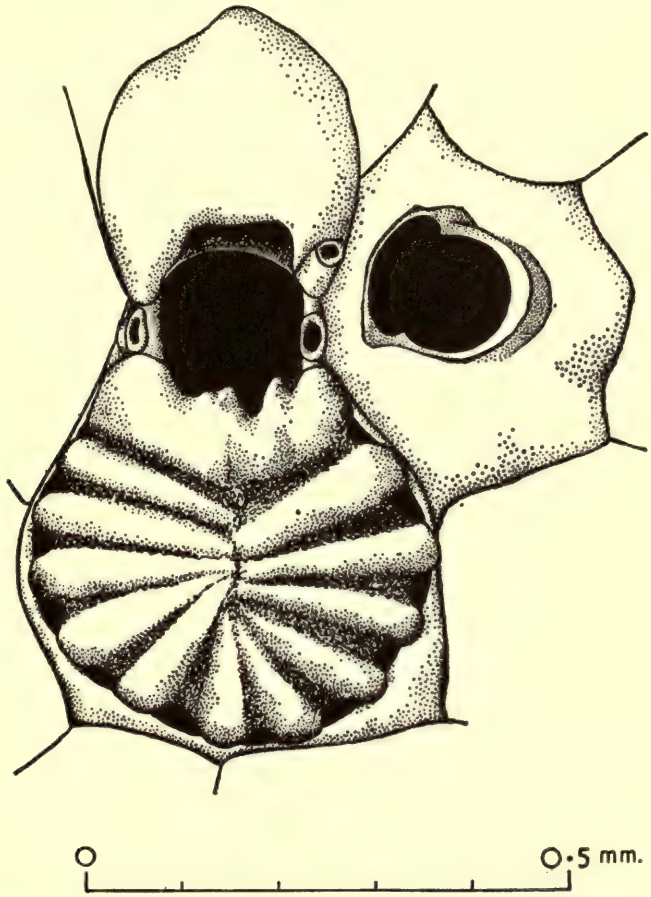


FIG. 38. *Lagynopora urceolus* Lang, D. 40944. Adult ovicelled zooecium and interzooecial avicularium. The proximal oral shield is destroyed ; the avicularium, with proximal-lateral constrictions, is directed typically outwards from the zooecium it accompanies.

Avicularia very prominent, larger than the orifice, interzooecial, directed just proximally and outwards from the zooecia they accompany, broadly oval with proximal-lateral constrictions dividing the wider semicircular proximal portion from the somewhat pointed longer *rostrum*. *Ovicells* very prominent, frequent, hyperstomial, large, smooth, globular, without *lateral slits*. *Young zooecia* similar to the adult zooecia, but smaller and with 5 or 6 oral spines and 12–16 costae. *Ancestrula* (of holotype) very small, with 7 oral spines. Number of costae unknown.

MEASUREMENTS. *Adult zooecia* Lz = 0·65 to 0·78 mm.
lz = 0·35 to 0·50 mm.
hr = 0·13 to 0·15 mm.
lr = 0·15 to 0·17 mm.
Avicularia Lz = 0·16 to 0·21 mm.
lz = 0·14 to 0·17 mm.
Young zooecia Lz = 0·35 to 0·47 mm.
lz = 0·23 to 0·30 mm.
hr = 0·10 mm.
lr = 0·10 to 0·12 mm.
Ancestrula (of holotype) Lz = 0·30 mm.
lz = 0·18 mm.
hr = 0·09 mm.
lr = 0·10 mm.

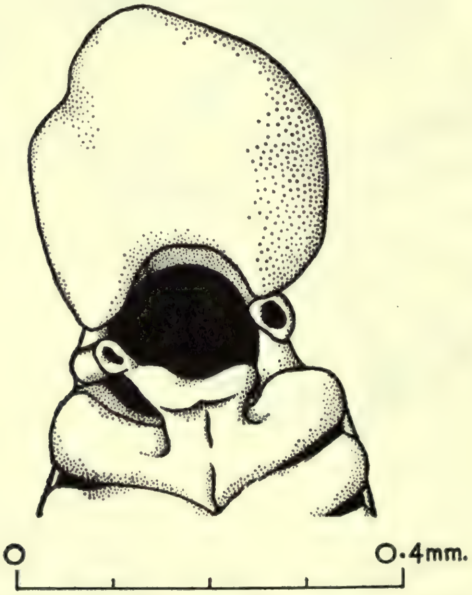


FIG. 39. *Lagynopora urceolus* Lang, D.28889. Holotype. Ovicell and orifice of adult zooecium with proximal oral shield broken on one side.

REMARKS. Lang (1921 : 65) apparently placed very little diagnostic value on the very distinctive avicularia of *L. urceolus* for he did not mention them in his diagnosis of the species. *L. urceolus* is distinguished particularly by its avicularia and to a lesser extent by the dimensions of its zooecia, its number of costae and its well-arched frontal shield.

The outline of individual costae may be traced across the median area of fusion which is narrow rather than " wide " as Lang has stated.

In D.40944, a well-preserved specimen, an avicularium is apparently replaced by a small, reversed, but otherwise normal zooecium.

Stratigraphical distribution. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*, and zone of *Marsupites*, subzone of *Uintacrinus*.

Specimens. D.28889. Holotype—see above.

D.29898. Ovicelled zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs west of Chimney Shaft, Roedean, east of Brighton, Sussex.

D.40944. Ovicelled zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.29898.

D.41064. *Lagynopora* cf. *urceolus*. Somewhat damaged ovicelled zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites*, subzone of *Uintacrinus*. Pit 49 of G. W. Young—Medical College Pit, Epsom, Surrey.

D.41067. Well-preserved, ovicelled zoarial fragment possibly close to part of the growing edge, encrusting a fragment of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Section 113 of Gaster, cliffs east of Rottingdean Gap to Saltdean, Sussex.

12. ***Lagynopora vasculum*** Lang

(Pl. 5, fig. 2 ; Text-figs. 40, 41)

1910 *Cribrilina furcifera* Brydone, p. 391 [*partim*—pl. 30, fig. 6 only ; *non* fig. 7 (= *Lagynopora furcifera*) ; *non* fig. 8 (= *L. ollula*)].

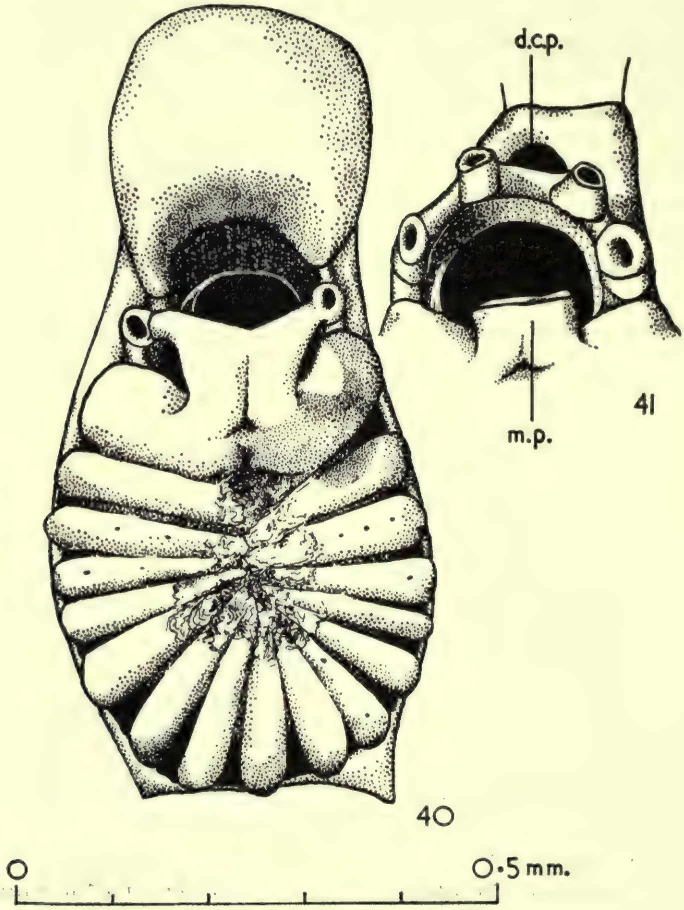
1916*a* *Lagynopora* [*Cribrilina*] *furcifera* (Brydone) : Lang, p. 395 [*partim*—Brydone, 1910, pl. 30, fig. 6 only].

1921 *Lagynopora vasculum* Lang, pp. xciii, 66, text-fig. 33.

Lectotype. (Chosen by Lang, 1921 : 67.) S.M., B.36164. A well-preserved zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Lower part of old pit and road cutting at Mount Pleasant, Andover, Hampshire. R. M. Brydone Collection.

Emended diagnosis. *Lagynopora* with large zooecia (Lz = 0·73 to 0·80 mm., lz = 0·45 to 0·50 mm.) ; proximal oral shield very prominent, obtusely " Y "-shaped ; median process of the apertural bar very wide ; costae numerous, 15–17, indistinct except towards the margins of the otherwise consolidated frontal shield ; intercostal spaces between the outer ends of the costae only ; ovicells hyperstomial, large, globular, smooth.

Description. *Zoarium* encrusting, unilaminar. *Adult zooecia* large, broadly oval, very closely placed, each with a large, prominent, round *distal communication pore* and two or more smaller, oval *lateral communication pores*. *Secondary orifice* wider than high, rounded distally and laterally with a straight proximal margin. *Oral spines* 4, arranged symmetrically round the orifice, the proximal-lateral pair slightly larger than the distal pair. *Proximal oral shield* very prominent, consisting of a very wide median process of the apertural bar ; the process bifurcates and fuses with the proximal-lateral pair of oral spines producing a very obtusely " Y "-shaped oral shield. The proximal oral shield when fully developed obscures most of the orifice. *Frontal shield* flatly arched. *Costae* 15–17, fairly narrow. At their outer ends the costae are separated by distinct *intercostal spaces* which extend about one-third of the distance towards the mid-line of the frontal shield. On either side of the mid-line a wide *median area of fusion* is developed, but the outlines of the inner ends of individual costae can be seen in this well-consolidated part of the frontal shield. Minute *pelmatidia* are visible on the upper surface of some unworn costae. No *lateral costal fusions*. No *median ridge* on the frontal shield. *Apertural bar* somewhat swollen, straight except for a slight distal bend at either end, wider than the most distal costae, with a strong, wide *median process* which forms part of the proximal oral shield. *Gymnocyst* smooth, only very occasionally exposed in small,



FIGS. 40, 41. *Lagynopora vasculum* Lang, S.M., B.36164. Lectotype.
(40) Adult ovicelled zooecium with complete proximal oral shield.
(41) Orifice of another adult zooecium in which the proximal oral shield is broken; *d.c.p.* distal communication pore in sloping distal wall of zooecium; *m.p*, median process of apertural bar.

triangular areas proximal to the frontal shields, generally obscured by the very close placing of the zooecia. No *interzooecial secondary tissue. Avicularia* are present occasionally. They are apparently interzooecial and fairly large, but in the lectotype only three worn avicularian-like structures have been seen. *Ovicells* hyperstomial, large, prominent, smooth, globular, occasionally slightly pointed distally, their proximal-lateral margins usually incorporating the distal pair of oral spines. *Young zooecia* smaller than the adult zooecia but otherwise similar. Only the first ring of young zooecia have 5 or 6 oral spines; all successive young and adult zooecia possess only 4 oral spines. *Ancestrula* (almost obscured in the lectotype), with 6 long, narrow oral spines.

MEASUREMENTS. *Adult zooecia* Lz = 0·73 to 0·80 mm.
lz = 0·45 to 0·50 mm.
hr = 0·12 to 0·15 mm.
lr = 0·15 to 0·18 mm.
?*Avicularia* Not measurable.
Young zooecia Lz = 0·43 to 0·46 mm.
lz = 0·30 mm.
hr = 0·10 to 0·11 mm.
lr = 0·11 to 0·12 mm.
Ancestrula Lz, lz, hr = Not measurable.
lr = 0·12 mm.

REMARKS. Lang (1921 : 66) based his diagnosis of *Lagynopora vasculum* on Brydone's figure of the species (1910, pl. 30, fig. 6). The median process of the apertural bar is much wider than is shown in Lang's text-figure 33 (1921 : 66), and the frontal shield is less consolidated.

As in *L. ollula* Lang, there is a rapid reduction in the number of oral spines during the growth of the zoarium, but, unlike *L. ollula*, this is apparently accompanied by a slight increase in the number of costae.

L. vasculum is distinguished mainly by its large size, its numerous costae, and the width of its median area of fusion which extends across about two-thirds of the frontal shield. Avicularia are apparently rare, contrasting with the prominent presence of avicularia in *L. ollula*.

See also remarks under *L. furcifera* (Brydone), p. 82.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*.

MATERIAL. S.M., B.36164. Lectotype—see above.

SPECIES OF UNCERTAIN SYSTEMATIC POSITION PREVIOUSLY ASSIGNED TO *LAGYNOPORA*

(1) ***Lepralia pediculus*** Reuss

1874 *Lepralia pediculus* Reuss, p. 129, pl. 24, fig. 16.
1921 [*Lagynopora*] *pediculus* (von Reuss) Lang, p. 61.

REMARKS. Lang himself (1921 : 61) regarded the systematic position of this species as uncertain, for he placed the name in square brackets and stated (p. 62)

" *Lepralia pediculus*, if a *Lagynopora*, appears to be closely related to *L. lagena* ; but the widely-spaced oecia [zooecia] at once distinguish it from that species ". In his diagnosis (1921 : 61) he described the species as a " [*Lagynopora*] of large size (oecia about ·66 mm. long) ; with about 16 closely-approximated costae ; lateral costal fusions rare or absent ; intraterminal front-wall [frontal shield] fairly well-arched ; oecia widely-spaced ".

This description was presumably based on that of Reuss (1874 : 129, pl. 24, fig. 16). There are no indications of lateral costal fusions in the figure, nor is there the slightest suggestion of a proximal oral shield—an essential generic character of *Lagynopora*. There is no evidence to suggest that *Lepralia pediculus* Reuss should be placed in *Lagynopora*. The spacing of the zooecia is not of diagnostic value, and Reuss's figure is very stylized showing, at the most, a multiserial cribrimorph polyzoan with a well-arched frontal shield, numerous costae, 6 or 7 oral spines, and hyperstomial, smooth, globular ovicells.

Gillard (1942 : 91) has referred a specimen from a boring at Montbazon, France, to " *Lagynopora pediculus* var. Reuss ". Its horizon may be Upper Turonian.

(2) ***Lagynopora ? prima*** (Kühn) nov. comb.

1930 *Canupora prima* Kühn, p. 65, pl. 26, fig. 13.
1935 *Canupora prima* Kühn : Bassler, p. 64.
1953 *Canupora prima* Kühn : Bassler, p. G188.

LECTOTYPE. (Here chosen.) The specimen figured by Kühn, 1930, pl. 26, fig. 13. Danian, Lithothamnienkalk. Haidhof, near Ernstbrunn, Austria.

DIAGNOSIS. (Based on Kühn's description and figure.) ?*Lagynopora* with encrusting zoarium ; zooecia of large size (Lz = 0·90 to 1·00 mm., lz = 0·56 to 0·58 mm.) ; orifice very large (hr = 0·28 mm., lr = 0·25 to 0·28 mm.), rounded distally and laterally with a straight proximal margin ; oral spines 6 ; frontal shield fairly well arched ; costae 8–11, separated for half their length by wide intercostal spaces ; median area of fusion extends about half-way along the costae ; apertural bar fairly wide, straight ; avicularia rare—their form unknown.

REMARKS. Kühn (1930 : 65) has commented " . . . our genus [*Canupora*] has great similarity to *Prodromopora* [= *Lagynopora*], but is distinguished by the presence of 6 oral spines, which is a more primitive condition than the 4 oral spines of *Prodromopora*, so that one may regard it as the most primitive genus of the Lagynoporidae. Always assuming that Lang's developmental series is correct " [translation].

It is difficult to interpret Kühn's figure, and in his description he did not state whether or not his material possessed proximal oral shields or large distal communication pores. The occurrence of 6 oral spines in the adult zooecia by no means justifies placing the species in a separate genus, and it is therefore provisionally referred to *Lagynopora*, especially as this, in its young stages, often has 6 oral spines. Also, if the age of the Lithothamnian Chalk is correctly established as Danian, it is very unlikely that *Lagynopora*? *prima* may be regarded as the most primitive unit in a developmental series of species which are otherwise confined to the Senonian.

No specimens of *Lagynopora*? *prima* are available in the collections of the British Museum (Natural History).

Genus *HEXACANTHOPORA* Lang

1916*a* *Hexacanthopora* Lang, p. 394.
1921 *Hexacanthopora* : Lang, pp. lxi, xcii, xciii, 44
1924 *Hexacanthopora* : Gaster, second of three tables opp. p. 110.
1927 *Hexacanthopora* : Canu & Bassler, pp. 17, 31.
1930 *Hexacanthopora* : Gaster, table opp. p. 340.
1930 *Hexacanthopora* : Voigt, pp. 495, 542, 560.
1935 *Hexacanthopora* : Bassler, pp. 30, 126.
1949 *Hexacanthopora* : Voigt, pp. 37, 43.
1953 *Hexacanthopora* : Bassler, p. G188.

TYPE SPECIES. *Hexacanthopora sexspinosa* Lang, 1916*a* : 394. Senonian, zone of *Marsupites* [subzone unspecified]. Roke Farm, south-east of Odiham, Hampshire. L. Treacher Collection.

EMENDED DIAGNOSIS. Pelmatoporinae with a small median process on the apertural bar—this process never fuses with the proximal-lateral oral spines to form a proximal oral shield ; oral spines often 6 ; avicularia large, prominent, often frequent.

REMARKS. *Hexacanthopora* Lang is distinguished from *Lagynopora* Lang primarily by the absence of a proximal oral shield, and from *Leptocheilopora* by the presence of a median process on the apertural bar and numerous, large avicularia.

Hexacanthopora is better distinguished on these characters than solely on the number of oral spines in its adult zooecia. Lang (1921 : 44) diagnosed *Hexacanthopora* as " Lagynoporinae [= Pelmatoporinae] in which (at least) some epheboecia [adult zooecia] have six apertural [oral] spines ". The genus may possess from 4 to 6 oral spines in the adult zooecia : in two specimens, D.28890 and D.29897, it was not possible to find any zooecium with 6 oral spines. It is, however, still true to say that the 4–6 (commonly 6) oral spines which occur in *Hexacanthopora* contrast with the number of oral spines in *Leptocheilopora*. In the latter there are 4 oral spines only, except in *L. vulnerata* (Brydone) where there are consistently 7 in each adult zooecium. *Lagynopora*, with the exception of *L. ollula* (4, occasionally 5) and *L.? prima* (6), consistently has only 4 oral spines in the adult zooecia.

Only two species of *Hexacanthopora* are recognized here : *H. sexspinosa* Lang, and *H. viginticostata* Voigt from the Senonian of Germany.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *M. cor-anguinum* to *B. mucronata*.

KEY TO THE SPECIES OF *HEXACANTHOPORA* LANG

(I) *Hexacanthopora* with 4–6 oral spines in the adult zooecia ; costae 11–18 ; median area of fusion not obscuring the inner ends of the costae ; avicularia usually frequent, of two sizes in the adult zoarial stage . . 1. ***H. sexspinosa*** Lang

(II) *Hexacanthopora* always with 6 oral spines in the adult zooecia ; costae 20 (average) ; median area of fusion wide, obscuring the outlines of the inner ends of the costae ; avicularia large, frequent, apparently of one size in the adult zoarial stage 2. ***H. viginticostata*** Voigt

1. *Hexacanthopora sexspinosa* Lang

(Pl. 5, figs. 3–6)

1916*a* *Hexacanthopora sexspinosa* Lang, p. 394.
1916*a* *Hexacanthopora kintburiensis* Lang, p. 394.
1916*a* *Hexacanthopora brightonensis* Lang, p. 394.
1921 *Hexacanthopora sexspinosa* Lang : Lang, lxi, xciii, 45, pl. 1, fig. 8 ; text-fig. 21.
1921 *Hexacanthopora kintburiensis* Lang : Lang, pp. xcii, 47, pl. 1, fig. 9 ; text-fig. 23.
1921 *Hexacanthopora brightonensis* Lang : Lang, pp. xcii, 48, text-fig. 24.
1924 *Hexacanthopora kintburiensis* Lang : Gaster, second of three tables opp. p. 110.
1924 *Hexacanthopora brightonensis* Lang : Gaster, second of three tables opp. p. 110.
1930 *Hexacanthopora sexspinosa* Lang : Gaster, table opp. p. 340.
1930 *Hexacanthopora kintburiensis* Lang : Gaster, table opp. p. 340.
1930 *Hexacanthopora brightonensis* Lang : Gaster, table opp. p. 340.
1930 *Hexacanthopora brightonensis* Lang : Voigt, pp. 495, 542, 560, pl. 26, fig. 11.
1930 *Hexacanthopora sexspinosa* Lang : Voigt, pp. 495, 542, 560, pl. 26, fig. 12.
1935 *Hexacanthopora sexspinosa* Lang : Bassler, p. 126.
1953 *Hexacanthopora sexspinosa* Lang : Bassler, p. G188, text-fig. 142, 11.

HOLOTYPE. D. 21205. Well-preserved zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites* [subzone unspecified]. Roke Farm, south-east of Odiham, Hampshire. L. Treacher Collection.

EMENDED DIAGNOSIS. *Hexacanthopora* with fairly large zooecia (Lz = 0·55 to 0·80 mm., lz = 0·35 to 0·55 mm.) ; orifice wider than high (hr = 0·10 to 0·15 mm., lr = 0·12 to 0·17 mm.) ; oral spines 4–6 ; costae 11–18, visible individually up to the mid-line of the frontal shield ; avicularia of two kinds, (*a*) a large oval form with small constrictions near the proximal end, (*b*) a smaller, similar form ; one type of avicularium may be more numerous than the other, or occasionally only one type may be visible, or, even more rarely, both types may be absent.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* fairly large, broadly oval, each with a very prominent, large *distal communication pore* and smaller *lateral communication pores*. *Dietellae* are present in the distal-basal angles of the zooecia, and revealed where the upper part of the zooecium has been worn away (see Pl. 5, fig. 3). *Orifice* wider than high, evenly rounded distally and laterally, with a straight or slightly proximally curved proximal margin. *Oral spines* 4–6, symmetrically arranged round the orifice. In a given zoarium 6 oral spines may be consistently developed in the adult zooecia, as in the holotype ; or 4, 5 or 6 oral spines may be present, as in D.21204 ; or only 4 or 5 may occur, as in D.28890. The proximal-lateral pair of oral spines are not enlarged as in *Lagynopora*. *Frontal shield* well arched, but flattened in the median area. *Costae* 11–18, separated for two-thirds of their length by distinct *intercostal spaces*. The costae are united in the median area of fusion, but the outlines of the inner ends of individual costae remain clearly visible. *Median area of fusion narrow*. Minute *pelmatidia* may be seen along the mid-line of well-preserved costae. *Apertural bar* straight, somewhat curved distally at either end, with a distinct, though fairly small, *median process* which apparently never fuses with the proximal-lateral pair of oral spines to form a proximal oral shield as in *Lagynopora*. *Gymnocyst* smooth, often slightly exposed proximally to the frontal shields and occasionally very narrowly along their sides. No *interzooecial secondary tissue.*

Avicularia of two sizes. Type *a* is a larger form, usually a little longer than wide, but occasionally the reverse is true, oval, or slightly pointed distally, with slight proximal-lateral constrictions dividing a small proximal portion from a very large *rostrum.* Tybe *b* is smaller, but otherwise similar to type *a*. Both types may be variously orientated—usually distally and very obliquely outwards from the zooecia they appear to accompany. None has been seen which is directed proximally. In a given zoarium one type or the other may be more frequent, or, very occasionally, only one form may be developed. Even more rarely avicularia may be absent.

Ovicells hyperstomial, prominent, globular, smooth, without *lateral slits.* A pair of oral spines may flank the entrance to the ovicell.

Young zooecia smaller than the adult zooecia, often with fewer (11–14) costae and more numerous oral spines. Paratype D.21207 possesses at least one young zooecium with 7 oral spines, and D.29895–96 have young zooecia with 6 oral spines and adult zooecia with only 4 or 5.

Ancestrula small, often obscured. In the holotype the ancestrula has 6 oral spines and 12 costae.

MEASUREMENTS. *Adult zooecia* Lz = 0·50 to 0·80 mm.
lz = 0·35 to 0·55 mm.
hr = 0·10 to 0·15 mm.
lr = 0·10 to 0·15 mm.
Young zooecia Lz = 0·35 to 0·50 mm.
lz = 0·21 to 0·33 mm.
hr = 0·09 to 0·11 mm.
lr = 0·10 to 0·13 mm.
Ancestrula (of holotype) Lz = 0·32 mm.
lz = 0·20 mm.
hr = 0·07 mm.
lr = 0·09 mm.
Avicularia :
Type *a* Lz = 0·18 to 0·25 mm.
lz = 0·17 to 0·25 mm.
Type *b* Lz = 0·11 to 0·18 mm.
lz = 0·09 to 0·16 mm.

REMARKS. *Hexacanthopora kintburiensis* Lang and *H. brightonensis* Lang are synonymous with *H. sexspinosa* Lang. Thirteen specimens of *Hexacanthopora,* labelled by Lang, are available in the collections of the British Museum (Natural History). Lang (1916*a* : 394 ; 1921 : 45) divided this material into three species, basing his division principally on the number of oral spines commonly developed in adult zooecia, the number of costae, and the length of zooecia. In addition he stated (1921 : 45) that *H. sexspinosa* possesses two types of avicularia, " both kinds, especially the smaller, rare ; the smaller kind are more or less distally directed, and have somewhat elongate, slightly constricted, and blunt apertures ; the larger vary in size, but generally have an aperture as large as that of an orthoecium [zooecium]; they are indifferently oriented, little longer than wide, with a somewhat pointed aperture divided by a constriction into a very much smaller proximal portion and a very large rostrum". The avicularia of *H. kintburiensis* he described (1921 : 47) as "occasional, large, with blunt, indifferently orientated apertures, nearly as large as those of the orthoecia, with a very slight constriction near the proximal end". *H. brightonensis* (1921 : 49) was stated to have "aviculoecia [avicularia] apparently of the large kind only, fairly numerous, irregularly distributed, with indifferently orientated, nearly circular apertures of nearly the same size as those of the orthoecia, and with a constriction nearer the proximal end".

Both large and small avicularia are, however, present in each of the species of *Hexacanthopora* recognized by Lang. The larger avicularia (type *a*) may be more numerous than the smaller (type *b*). Normally avicularia occur infrequently, but in one specimen, D.28890—the holotype of *H. brightonensis* Lang, they are unusually abundant.

The type and variable number of the avicularia do not aid specific division of the material. Similarly the dimensions of the zooecia and the ranges in number of costae, in the three species recognized by Lang, overlap or are the same. These characters and the number of oral spines are compared in the following table:

Specimens labelled by Lang as:	Measurements in mm.			
	Lz	lz	hr	lr
1. *H. sexspinosa*	0·55 to 0·75	0·35 to 0·45	0·10 to 0·13	0·12 to 0·15
2. *H. kintburiensis*	0·55 to 0·80	0·35 to 0·55	0·10 to 0·15	0·14 to 0·17
3. *H. brightonensis*	0·60 to 0·67	0·38 to 0·50	0·13	0·15

	Costae	Oral spines
1.	14–18	6
2.	11–18	4–6
3.	11–13	4–5

All adult zooecia in the specimens labelled by Lang "*H. sexspinosa*" possess 6 oral spines, whereas those labelled "*H. kintburiensis*" have adult zooecia with 4 or 5 as well as commonly 6 oral spines. In the specimens labelled "*H. brightonensis*" a few adult zooecia have only 4 oral spines, the majority have 5 and no definite instance could be found of 6 oral spines.

Voigt (1930 : 495) has recorded specimens of *H. sexspinosa* and *H. brightonensis* from Germany in chalk equivalent in age to the zones of *Marsupites* and *G.* [*A.*] *quadrata*.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *Marsupites* to *G.* [*A.*] *quadrata* in England and Germany, ?also zone of *M. cor-anguinum* in England.

SPECIMENS. D.21205. Holotype—see above.

D.21206. Paratype. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for the holotype.

D.21207. Paratype. Zoarial fragment with ancestrula and mainly young zooecia encrusting a piece of echinoid test. Senonian, ? zone of *Marsupites*. Odiham, Hampshire. L. Treacher Collection.

D.29101. Paratype. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites* [subzone unspecified]. Margate, Kent. N. T. Wetherell Collection.

D.21204. Holotype of *Hexacanthopora kintburiensis* Lang. Well-preserved zoarium, two zooecia with undamaged ovicells, encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata.* Kintbury, west of Newbury, Berkshire. L. Treacher Collection.

D.29070. Paratype of *H. kintburiensis* Lang. Zoarial fragment encrusting a piece of ?*Inoceramus* shell. Senonian, zone of *G.* [*A.*] *quadrata.* Romsey, south-west of Winchester, Hampshire. H. P. Blackmore Collection.

?D.2631 Paratype of *H. kintburiensis* Lang. A worn zoarial fragment with about ten abraded zooecia only. It is not possible to distinguish the number of oral spines, nor to measure the orifice. Encrusting a shell fragment. Upper Senonian [zone unspecified]. Salisbury, Wiltshire. G. R. Vine Collection.

D.28890. Holotype of *H. brightonensis* Lang. Zoarial fragment with fairly well preserved zooecia and very frequent avicularia, encrusting a piece of echinoid test. Senonian, zone of *Marsupites* [subzone unspecified]. Brighton, Sussex.

?D.28891. Paratype of *H. brightonensis* Lang. A very small, worn zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *depressula.* Cliffs between last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.

D.29896. Zoarial fragment with ancestrula and numerous adult ovicelled zooecia. Encrusting a piece of echinoid test. Labelled by Lang " *H. kintburiensis* ". Senonian, zone and subzone of *Marsupites.* West pit, in top of Hangleton Lane, Highdown Hill, east of Angmering, Sussex.

?D.21208. Very poorly preserved zoarial fragment encrusting a piece of echinoid test. Labelled by Lang " *H. kintburiensis* ". Senonian, zone of *M. coranguinum.* Woburn Green, south-west of Beaconsfield, Buckinghamshire. L. Treacher Collection.

D.29895. Zoarial fragment with ancestrula and adult ovicelled zooecia encrusting a piece of echinoid test. Labelled by Lang " *H. kintburiensis* ". Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *depressula.* Pit 4 of Gaster, western pit, south of Lancing Ring and west of Boundstone Lane, north-east of Worthing, Sussex.

D.29897. Worn zoarial fragment with obscured ancestrula. Encrusting a piece of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *depressula.* Cliffs, west of Chimney Shaft, Roedean, east of Brighton, Sussex.

D.41065. Very small zoarial fragment with young zooecia encrusting a piece of echinoid test. Senonian, zone and subzone of *Marsupites.* Section 75 of Gaster, Brighton Cliffs, Sussex.

2. *Hexacanthopora viginticostata* Voigt

1930 *Hexacanthopora viginticostata* Voigt, pp. 495, 560, pl. 26, fig. 13.
1949 *Hexacanthopora viginticostata* Voigt : Voigt, pp. 37, 43, pl. 9, figs. 1, 2.

NEOTYPE. (Designated by Voigt, 1949 : 37, pl. 9, fig. 2.) Sample 142. Senonian, zone of *G.* [*A.*] *quadrata*. Lägerdorf, Holstein, Germany.

DIAGNOSIS. (Based on Voigt's descriptions and figures, 1930; 1949.) *Hexacanthopora* with zooecia of fairly large size (Lz = 0·60 to 0·70 mm., lz = about 0·40 mm.) ; orifice small, higher than wide (hr = about 0·12 mm.) ; oral spines constantly 6 ; costae 20 (average) ; median area of fusion wide, obscuring the outlines of the inner two-thirds of the costae ; avicularia variable in occurrence, large (0·20 to 0·30 mm. diameter), with a slit-like or irregularly polygonal aperture, smaller in the young than in the adult stages of zoarial growth ; ovicells hyperstomial, large, globular ; young zooecia with fewer (about 14–16) costae ; ancestrula about 0·30 mm. long.

REMARKS. Voigt recently (1949 : 37) designated a neotype for the species, the holotype having been lost in a fire. The well-preserved new material, from the same horizon and the same and different localities as the original specimens, differs mainly in the number of avicularia present. They are apparently much more numerous than in the original material in which they were " rare ".

H. viginticostata Voigt is distinguished from *H. sexspinosa* Lang by its larger number of costae and its wide median area of fusion. Also the orifice of the former is apparently higher than wide, contrasting with that of *H. sexspinosa* which is consistently wider than high.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *G.* [*A.*] *quadrata* and *B. mucronata* in Germany.

SPECIMENS. None in the collections.

Genus *LEPTOCHEILOPORA* Lang

?1852 *Reptoporella* d'Orbigny, pl. 717, figs. 6, 7 ; 1853, p. 474 ; 1854, p. 1097.
?1857 *Repteporella* [*sic*] : Pictet, p. 111.
1900*b* *Cribrilina* (*Typica*) : Canu, p. 447 [*partim*].
1900*b* *non Membranipora* : Canu, p. 449.
1910 *Cribrilina* : Brydone, p. 391 [*partim*].
1912 *Cribrilina* : White, p. 43 [*partim*].
1914*b* *Cribrilina* : Brydone, p. 97 [*partim*].
1916*a* *Leptocheilopora* Lang, p. 396.
1917 *Cribrilina* : Brydone, p. 51 [*partim*—*C. tumuliformis* only].
?1917 *Reptoporella* : Lang, p. 172.
1917 *Leptocheilopora* : Lang, p. 172.
1921 *Leptocheilopora* : Lang, pp. lxii, lxv, 68.
?1921 *Reptoporella* : Lang, p. lxv.
1925 *Barroisina* : Levinsen, p. 384 [*partim*—*B. galeata* only].
1930 *Leptocheilopora* : Voigt, p. 496.
1930 *Leptocheilopora* : Gaster, table opp. p. 340.
1935 *Leptocheilopra* : Bassler, pp. 30, 138.
1943 *Leptocheilopora* : Gillard, pp. 186, 187 [probably *partim*—? *non L. regularis* (d'Orbigny)].
1953 *Leptocheilopora* : Bassler, p. G188.

TYPE SPECIES. *Leptocheilopora tenuilabrosa* Lang, 1916*a* : 397. Senonian, zone of *Marsupites testudinarius* (subzone unspecified). Brighton, Sussex.

EMENDED DIAGNOSIS. Pelmatoporinae with no median process on the apertural bar; no proximal oral shield; avicularia absent or only very occasionally developed.

REMARKS. Lang (1921 : 71), followed by Bassler (1953 : G188), suggested that *Reptoporella* d'Orbigny may be a synonym of *Leptocheilopora* Lang, but this cannot be decided until d'Orbigny's material of *Reptoporella regularis* d'Orbigny (1853 : 475, pl. 717, figs. 6, 7), the type species of *Reptoporella*, has been restudied. (See discussion of species of uncertain systematic position p. 118.)

Leptocheilopora as here defined is placed in the subfamily Pelmatoporinae. Four species are recognized: *L. magna* Lang and *L. vulnerata* (Brydone) are, as yet, known only from the Lower Maastrichtian or highest Senonian, *L. filliozati* (Brydone) occurs throughout the zones of *G.* [*A.*] *quadrata* and *O. pilula*, and *L. tenuilabrosa* Lang is recorded from the zones of *Marsupites* and *Micraster cor-anguinum*.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum* to zone of *B. mucronata*, and Maastrichtian, zone of *Ostrea lunata* in England, zone of *Belemnella lanceolata* mut. *sumensis* or zone of *B. junior* in Germany.

KEY TO THE SPECIES OF *LEPTOCHEILOPORA*

(I) *Leptocheilopora* with zooecia of large size (Lz = 0·80 to 1·00 mm., lz = 0·50 to 0·66 mm.); orifice of constant form with marked proximal-lateral constrictions . . . 1. **L. magna** Lang

(II) *Leptocheilopora* with zooecia of small size (Lz = less than 0·75 mm.).

- (A) Primary ovicells costate; costae 17–22, (11–15 in young zooecia); intercostal spaces distinct; apertural bar broadly triangular, usually somewhat curved proximally; large, vicarious, spatulate avicularia may occur in the adult stages of some zoaria . . . . 2. **L. tenuilabrosa** Lang
- (B) Primary ovicells smooth.
  - (1) Lz = 0·55 to 0·75 mm., lz = 0·35 to 0·55 mm.; orifice of variable shape, but often with proximal-lateral constrictions (hr = 0·12 to 0·17 mm., lr = 0·12 to 0·16 mm.); oral spines 4; costae 12–18, well defined; often with a median ridge on the frontal shield; ovicells without lateral slits . . . . 3. **L. filliozati** (Brydone)
  - (2) Lz = 0·42 to 0·50 mm., lz = 0·31 to 0·35 mm.; orifice small, of fairly constant size (hr = 0·10 to 0·12 mm., lr = 0·09 to 0·11 mm.); usually lacking proximal-lateral constrictions; oral spines 7; frontal shield flatly arched without a median ridge; costae 11–15, flat, closely placed; ovicell with small lateral slits . . . . 4. **L. vulnerata** (Brydone)

Reptoporella regularis d'Orbigny, previously assigned to *Leptocheilopora*, and *Leptocheilopora longuessensis* Lang are of uncertain systematic position and are omitted from the above key.

1. *Leptocheilopora magna* Lang

(Pl. 6, figs. 1–7; Text-figs. 42, 43)

1916*a* *Leptocheilopora magna* Lang, p. 396.
?1916*a* *Leptocheilopora languessensis* [*sic*] Lang, pp. 396, 397.

?1921	*Leptocheilopora longuessensis* Lang: Lang, p. 76.
1921	*Leptocheilopora magna* Lang: Lang, p. 77, pl. 2, fig. 9; text-fig. 38.
1925	*Barroisina galeata* Levinsen, p. 385, pl. 6, fig. 67.
1930	*Leptocheilopora magna* Lang: Voigt, p. 496 [*partim*], pl. 27, fig. 5 [probably *non* fig. 4].

HOLOTYPE. D.19623. Incomplete zoarium with ancestrula, encrusting a fragment of echinoid test. Horizon given as " Senonian, Campanian, zone of *B. mucronata*, Lüneburg, Hanover ", Germany—very probably Maastrichtian. F. Möckler Collection.

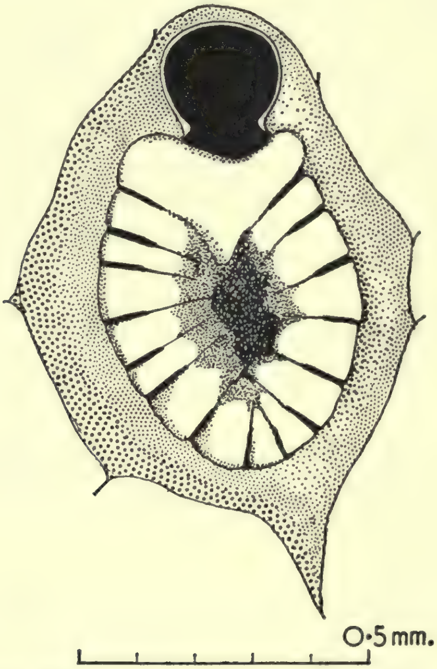


FIG. 42. *Leptocheilopora magna* Lang, D.38919. Adult zooecium with widely exposed gymnocyst and marked proximal-lateral constrictions in the orifice.

EMENDED DIAGNOSIS. *Leptocheilopora* with zooecia of large size (Lz = 0·80 to 1·00 mm.); costae 12–17; orifice with marked proximal-lateral constrictions.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* large, broadly oval, each with a single, fairly large, *distal communication pore*. *Orifice* higher than wide, rounded distally and laterally with marked proximal-lateral constrictions, the proximal margin often well curved proximally. *Oral spines* 4, small, unmodified. *Frontal shield* wide and flat. *Costae* 12–17, flat, tapering inwards where their distal ends may be traced across the wide *median area of fusion*. No *lateral costal fusions*. Very small *pelmata*, usually obscured by wear, along the mid-line of each costa. *Apertural bar* usually a little wider than the most distal costae, flat, smooth and curved proximally, with no median process. *Gymnocyst* often almost obscured by the close placing of the zooecia, but usually visible proximally to the frontal shield, and occasionally widely exposed all round the frontal shield (Text-fig. 42). No *interzooecial secondary tissue.*

Avicularia absent. *Primary ovicells* large, prominent, hyperstomial, smooth, globular, apparently composed of a smooth endooecium and a costate ectooecium which is usually incomplete and marginal. *Young zooecia* small, with only 10 costae. The orifice lacks the proximal-lateral constrictions characteristic of the orifices of adult zooecia, and is less markedly higher than wide. Oral spines 4, more prominent than in the adult zooecia. Frontal shield flatly arched, with only a very small amount of gymnocyst exposed proximally to it.

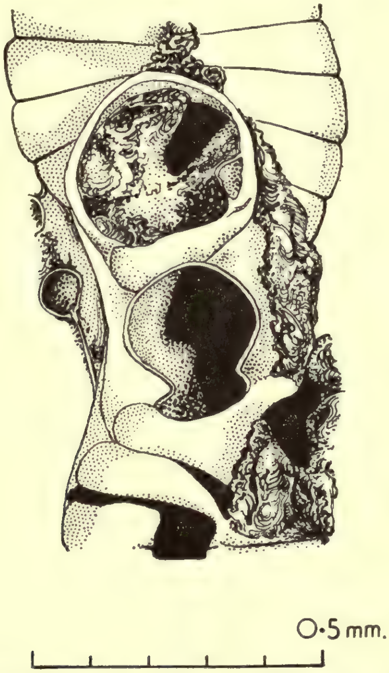


Fig. 43. *Leptocheilopora magna* Lang, D.38918. Orifice and broken ovicell resting on the proximal part of frontal shield of succeeding zooecium. The specimen is partly obscured by matrix.

Measurements. *Adult zooecia* Lz = 0·80 to 1·00 mm.
lz = 0·50 to 0·66 mm.
hr = 0·21 to 0·24 mm.
lr = 0·18 to 0·21 mm.
Young zooecia Lz = 0·50 mm.
lz = 0·27 mm.
hr = 0·15 mm.
lr = 0·12 mm.

REMARKS. The holotype, D.19623, and paratype, D.19622, have been re-examined. The former has the ancestrula imperfectly preserved, and outside the first ring of zooecia the range in number of costae, 12–17, is the maximum yet recorded for *L. magna*. In this specimen the measurements are: Lz = 0·90 to 1·00 mm., lz = 0·56 to 0·66 mm., hr = 0·21 mm., lr = 0·18 mm. The dimensions of the orifice are very constant. All zooecia of the holotype are apparently non-ovicelled.

Paratype D.19622 is a much damaged and worn zoarium with only the ancestrula and surrounding rings of young zooecia preserved; the majority of the zooecia are thus small.

Two specimens, D.38918 and D.38919, labelled by Voigt as *L. magna* Lang, have also been re-examined. The zooecia of the former are slightly larger and possess a few more costae than those of the latter. Imperfectly preserved ovicells are present in both specimens.

Voigt (1930 : 496, pl. 27, figs. 4, 5) assigned two specimens to *L. magna* Lang. I accept the specimen shown in fig. 5 as belonging to the species, but that shown in fig. 4 has a very marked series of short, slot-like intercostal spaces, a feature which I have not found in the specimens of *L. magna* available to me. I have therefore tentatively excluded that specimen from the synonymy of the species.

In agreement with Voigt (1930 : 496), *Barroisina galeata* Levinsen is regarded as synonymous with *Leptocheilopora magna* Lang. Levinsen (1925 : 385, pl. 6, fig. 67) referred to the " rib area [frontal shield] . . . of 7–9 pairs of flat ribs ", to its " high, rounded, strongly arched " ovicells, and to the absence of avicularia—all characteristic of *L. magna*.

The imperfectly preserved ovicells which occur in D.38918 and D.38919 are apparently ribbed or costate marginally, and seem to consist of two layers interpreted as a smooth endooecium partly covered by a costate ectooecium. The primary ovicell of *L. magna* Lang is smooth, but this primary layer (the endooecium) may be partly covered secondarily by an outer layer (the costate ectooecium). This feature could lead to confusion with *L. tenuilabrosa* Lang, in which the primary ovicell is costate, consisting of one layer only. However, the very large size of *L. magna* Lang and its very distinctively shaped orifice (pliophloean)[1] serve to distinguish it clearly from other species of *Leptocheilopora*.

Leptocheilopora longuessensis Lang is provisionally included in the synonymy of *L. magna* Lang. The diagnoses given by Lang (1916*a* : 396 ; 1921 : 76) are based only on the interpretation of a poor photograph of the holotype in the Canu Collection. From the photograph it is possible to determine only that the zoarium is that of an encrusting, unilaminar *Leptocheilopora*; the zooecia are broadly oval with flatly arched frontal shields possessing fairly numerous (probable about 16) costae; the orifice is longitudinally elongate and distally and laterally rounded with proximal-lateral constrictions and 4 somewhat enlarged oral spines. It is very probable that the zooecia shown in the photograph are close to the ancestrula, as those near the base of the zoarial fragment are much smaller than those near the outer edges. This being so it is very uncertain whether the smaller size of the zooecia can have much diagnostic significance—Lang (1921 : 76) gave Lz as about 0·60 mm. and lz as 0·48 mm. The specimen could well be part of the young stage of zoarium of *Leptocheilopora magna* Lang. However, this opinion can only be tentative.

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[1] See Lang, 1921 : xlvii, fig. 109.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian, either zone of *Belemnella lanceolata* mut. *sumensis* or zone of *B. junior,* and Senonian, zone of *Belemnitella mucronata.*

SPECIMENS. D.19623. Holotype—see above.

D.19622. Paratype. Damaged and worn zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for the holotype.

D.38918. Zoarial fragment encrusting a piece of siliceous sponge. Maastrichtian, either zone *Belemnella lanceolata* mut. *sumensis* or zone of *B. junior.* Cement factory (loose on floor), Hemmoor, Hanover, Germany. E. Voigt Collection.

D.38919. Zoarial fragment encrusting a belemnite guard. Horizon, locality and collection as for D.38918.

D.39431. Two damaged zooecia only, encrusting a fragment of echinoid test. Senonian, zone of *Belemnitella mucronata.* Felpham Chalk [foreshore], Bognor, Sussex.

2. ***Leptocheilopora tenuilabrosa*** Lang

(Pl. 6, figs. 8–11 ; Pl. 7, figs. 1, 2 ; Text-figs. 44–48)

1916*a*	*Leptocheilopora tenuilabrosa* Lang. pp. 396 397.
1917	*Leptocheilopora tenuilabrosa* Lang : Lang p. 172.
1917	*Cribrilina tumuliformis* Brydone, p. 51, pl. 3, figs. 7, 8.
1921	*Leptocheilopora tenuilabrosa* Lang : Lang, pp. lxii, xciii, 73, pl. 2, fig. 7 ; text-fig. 35.
1921	*Leptocheilopora gasteri* Lang, pp. xciv, 71, pl. 2, fig. 6 ; text-fig. 34.
1930	*Leptocheilopora tenuilabrosa* Lang : Gaster, table opp. p. 340.
1935	*Leptocheilopora tenuilabrosa* Lang : Bassler, p. 138.
1953	*Leptocheilopora tenuilabrosa* Lang : Bassler, p. G188, text-fig. 142, 10.

HOLOTYPE. D.28892. Zoarial fragment, probably with fairly young zooecia, encrusting a piece of echinoid test. Senonian, zone of *Marsupites testudinarius* (subzone unspecified). Brighton, Sussex.

EMENDED DIAGNOSIS. *Leptocheilopora* with costate primary ovicell ; costae 17–22, (11–15 in younger zooecia) ; intercostal spaces distinct ; large, spatulate, vicarious avicularia may occur in the adult stages of some zoaria.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, with a single, oval *distal communication pore. Orifice* small, of variable shape ; always rounded distally and usually rounded laterally, but occasionally with straight sides, and often with slight, but distinct, proximal-lateral constrictions ; proximal margin straight or slightly curved proximally. A distinct median notch, probably produced by wear, may be present in the proximal margin of the orifice. *Oral spines* 4, very small, indistinct, grouped on the distal margin of the orifice. *Frontal shield* flatly arched, the costae curving down gently from the mid-line to meet the gymnocyst. *Costae* 17–22, flat, tapering inwards, and separated by narrow, but distinct, *intercostal* *spaces.* No *lateral costal fusions.* Very small *pelmata* occur along the mid-line of the upper surface of each costa. *Apertural bar* straight, or slightly curved proximally when it is very broadly triangular (the apex of the triangle directed proximally), flat, with no *median process*, and only slightly wider than the distal costae ; a very slight median ridge may be present and this may be prolonged on to the frontal shield as an irregular median ridge. *Gymnocyst* smooth, usually well exposed, except where the close placing of zooecia may obscure it. No *interzooecial secondary tissue.*

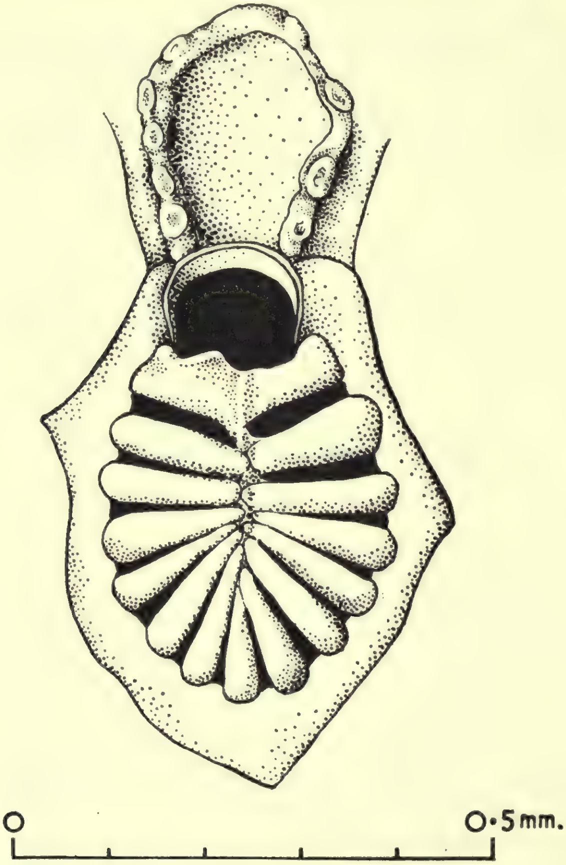


FIG. 44. *Leptocheilopora tenuilabrosa* Lang, D.28892. Holotype. Adult zooecium with broken, worn, costate ovicell ; the apertural bar is slightly damaged.

Avicularia very large, occasional, sporadic, vicarious and spatulate with costate frontal shields covering the proximal part of the aperture (about 8–13 costae are present). The distal end of the spatulate *rostrum* may include a narrow calcareous shelf (Text-fig. 47), but, in some cases, this may be absent (Text-fig. 48). Avicularia have been seen only in the adult stages of two zoaria : they apparently do not occur in the younger stages of zoarial growth and may be absent even in the adult zones of a zoarium. *Primary ovicells* prominent, frequent, hyperstomial, costate, tending to be longer than wide. The 11–13 flat, hollow costae which cover the ovicell apparently possess occasional minute pores along their mid-lines: the costae may form an *ectooecium*, but this is uncertain. *Young zooecia* smaller than the adult zooecia, with fewer (11–15) costae, and apparently not associated with vicarious avicularia.

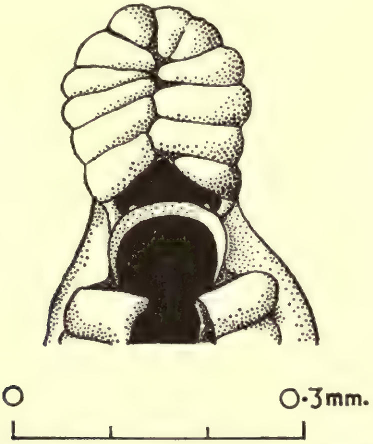


FIG. 45. *Leptocheilopora tenuilabrosa* Lang, D. 28892. Holotype. Orifice and complete costate ovicell of adult zooecium; the apertural bar is broken in the middle.

MEASUREMENTS. *Adult zooecia* Lz = 0·57 to 0·66 mm.
lz = 0·32 to 0·50 mm.
hr = 0·12 to 0·13 mm.
lr = 0·13 t9 0·14 mm.
Avicularia Lz = 0·80 to 0·83 mm.
lz = 0·33 to 0·36 mm.
Young zooecia Lz = 0·43 to 0·52 mm.
lz = 0·30 to 0·45 mm.
hr = 0·08 to 0·10 mm.
lr = 0·10 to 0·12 mm.

REMARKS. *Leptocheilopora gasteri* Lang is synonymous with *L. tenuilabrosa* Lang. The only apparent difference between the two species, which may be established on the specimens available in the collections of the British Museum (Natural History), is in the range in number of costae: 16–18 for the former and 11–15 for the latter. The dimensions of the zooecia, and particularly of the orifices, are very similar and both species have costate ovicells. Lang (1921 : 71, 72) mentioned and figured what he regarded as "rather obvious, irregular lateral costal fusions" in *L. gasteri*. The available specimens labelled by him as *L. gasteri* are worn, but the costae are clearly separated by narrow slit-like intercostal spaces (Text-fig. 46). Uneven wear, possibly combined with a certain amount of secondary calcification during fossilization, has apparently produced small hollows and slight, irregular accumulations of calcium-carbonate in the narrow spaces between the costae. These might easily be misinterpreted as incipient lateral costal fusions The same feature occurs occasionally in the specimens which he assigned to *L tenuilabrosa*

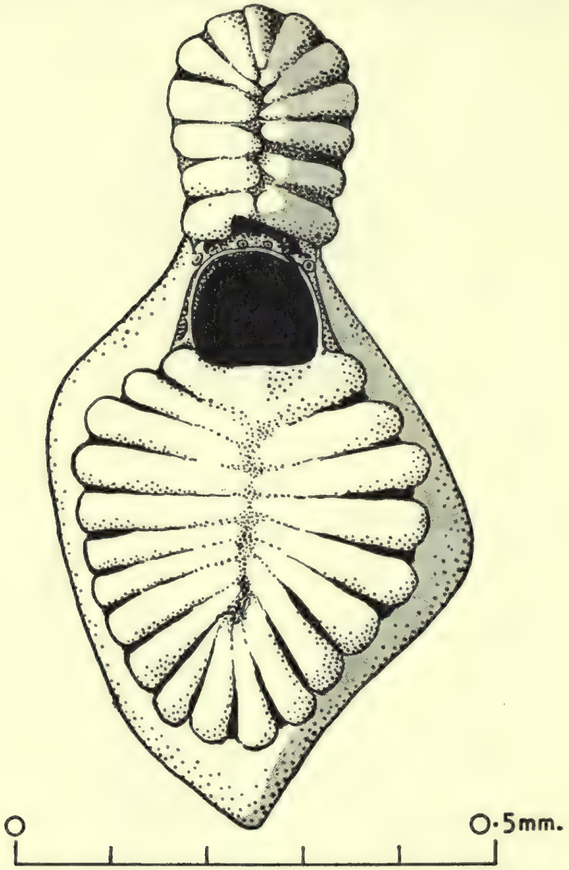
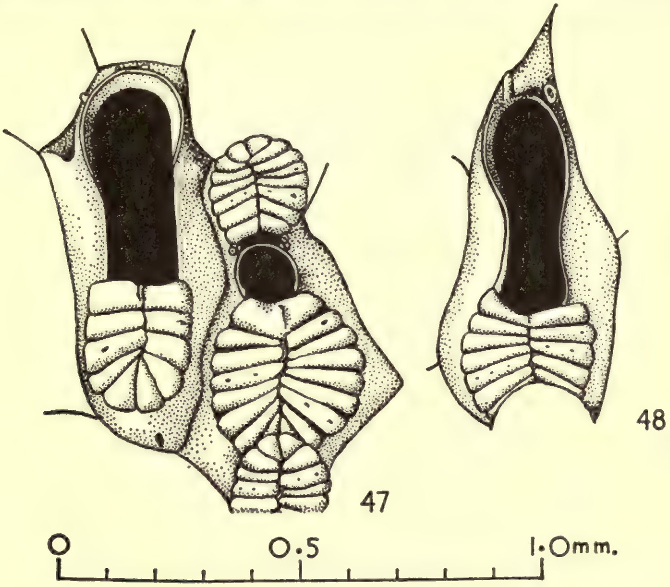


FIG. 46. *Leptocheilopora tenuilabrosa* Lang, D.29901. Holotype of *L. gasteri* Lang. Adult zooecium with costate ovicell, with four minute oral spine-bases grouped on distal margin of orifice.

Lang (1921 : 73) regarded *Cribrilina tumuliformis* Brydone (1917 : 51, pl. 3, figs. 7, 8) as synonymous with *Leptocheilopora tenuilabrosa*. Examination of Brydone's figured specimens of *Cribrilina tumuliformis* confirms this opinion. The range in number of costae in Brydone's specimens, S.M., B.36338–39, is, however, 17–22, and in both zoaria large, spatulate, vicarious avicularia are present. Young zooecia are also preserved and these are more closely similar to the zooecia of the holotype of *L. tenuilabrosa* (D.28892) and to those of the paratype (D.21210) than are the adult zooecia. It seems probably that Lang's specimens lack the fully developed adult stages of zoarial growth. In S.M., B.36339 a complete but small normal zooecium is regenerated inside a larger, damaged individual.

The very unusual vicarious, costate avicularia which may be present are particularly diagnostic of *L. tenuilabrosa*. Even where avicularia are absent, as they may be in some zoaria, the costate primary ovicell clearly distinguishes the species. Dr. Hastings kindly sent me the following note: "Vicarious avicularia with a costulate frontal shield are found in some recent species of *Figularia*. I have seen them in the type material of *F. philomela* Busk sp., where they were also observed by Harmer (1902 : 239); and in the specimen of *F. spatulata* (Calvet) collected by the *Discovery* Expedition (Stat. 47, 1 mile west of Shag Rocks, South Georgia, 199 m.)." Osburn (1950, p. 188, pl. 29, fig. 1) described and figured a new Recent species, *Colletosia bellula*, in which "the primary ovicell is small . . . smooth . . .; it soon becomes covered by an ectooecium which is composed of three or four pairs of radiating costules similar to those of the front and with similar lacunae [intercostal spaces]. . . ."



FIGS. 47, 48. *Leptocheilopora tenuilabrosa* Lang.

(47) S.M., B.36339. Figured Brydone (1917, pl. 3, fig. 8) as *Cribrilina tumuliformis*. Adult zooecium with costate ovicell (the ovicell of the preceding zooecium is also shown covering the proximal end of the zooecium) and a large, vicarious avicularium with costate frontal shield.

(48) S.M., B.36338. Figured Brydone (1917, pl. 3, fig. 7) as *Cribrilina tumuliformis*. Vicarious avicularium with typically spatulate rostrum and costate frontal shield. Small spine-bases may occur near the distal end of the aperture.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *M. cor-anguinum* and *Marsupites*.

SPECIMENS. D.28892. Holotype—see above.

D.21210. Paratype. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites* [subzone unspecified]. Roke Farm, south-east of Odiham, Hampshire. L. Treacher Collection.

D.29901. Holotype of *L. gasteri* Lang. Zoarial fragment encrusting a piece of *Inoceramus* shell. Senonian, zone of *M. cor-anguinum*. Pit in Houndean Bottom, west of Lewes, Sussex.

D.29902. Paratype of *L. gasteri* Lang. Zoarial fragment encrusting a piece of *Inoceramus* shell. Horizon, locality and collection as for D.29901.

D.40931. Another fragment of D.29902.

OTHER MATERIAL

S.M., B.36338. Large, well-preserved zoarial fragment, encrusting a piece of echinoid test. Figured by Brydone (1917, pl. 3, fig. 7) as *Cribrilina tumuliformis*. Senonian, zone of *M. cor-anguinum*. Leaves Green, Kent. R. M. Brydone Collection.

S.M., B.36339. Large, well-preserved zoarial fragment encrusting a piece of echinoid test. Figured by Brydone (1917, pl. 3, fig. 8) as *Cribrilina tumuliformis*. Senonian, horizon and collection as for S.M., B.36338. Gravesend, Kent.

3. ***Leptocheilopora filliozati*** (Brydone)

(Pl. 7, figs. 3, 4; Pl. 8; Text-figs. 49, 50)

1910 *Cribrilina filliozati* Brydone, p. 391, pl. 30, figs. 9, 10.
1912 *Cribrilina filliozati* Brydone : White, p. 43.
1916*a* *Leptocheilopora filliozati* (Brydone) Lang, p. 396.
1916*a* *Leptocheilopora arcuata* Lang, pp. 396, 397.
1921 *Leptocheilopora filliozati* (Brydone) : Lang, pp. xcii, 76.
1930 *Leptocheilopora arcuata* Lang : Gaster, table opp. p. 340.
1930 *Leptocheilopora filliozati* (Brydone) : Gaster, table opp. p. 340.
1943 *Leptocheilopora arcuata* Lang : Gillard, p. 187.

LECTOTYPE. (Chosen by Lang, 1921 : 77.) S.M., B.36167, the specimen figured by Brydone, 1910, pl. 30, fig. 9. Zoarium, with ancestrula, encrusting a fragment of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Locality 932 of Brydone, lower part of old pit and road cutting at Mount Pleasant, on the road to Micheldever, Andover, Hampshire. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Leptocheilopora* with zooecia of variable size (Lz = 0·55 to 0·75 mm., lz = 0·35 to 0·55 mm.) ; orifice of variable shape but usually with proximal-lateral constrictions ; frontal shield fairly well arched with 12–18 well-defined costae and often with a median ridge ; ovicells smooth, without lateral slits.

DESCRIPTION. *Zoarium* unilaminar, encrusting. *Adult zooecia* broadly oval, closely placed. A large *distal communication pore* and two or three round *lateral communication pores* are present. *Orifice* always slightly higher than wide, of fairly constant dimensions, rounded distally and laterally, with proximal-lateral constrictions present but seldom pronounced as in *Leptocheilopora magna*, proximal margin usually gently curved proximally. The shape of the orifice varies proximally, where the proximal-lateral constrictions may not be distinct and the proximal margin may vary from straight to proximally curved or, occasionally prominently " V "-shaped: the absence of the constrictions may be due to wear. *Oral spines* 4, slightly thickened, equally spaced on the margin of the orifice. *Frontal shield* gently arched. *Costae* 12–18, distinct, but often very closely placed, rounded at their outer ends and tapering inwards where they may be traced across the *median area of fusion* which is of variable width. No *lateral costal fusions*. In well-preserved specimens some costae show three (possibly four) very small *pelmata* along their mid-line. This feature is easily obscured by wear and possibly also by deposition of calcium-carbonate during fossilization, and may thus not be visible. *Apertural bar* often " V "-shaped, the apex pointing proximally, not much wider than the distal costae, smooth except for a slight median ridge which is often prolonged down the mid-line of the frontal shield. *Gymnocyst* not much exposed laterally, but often visible proximally to each frontal shield. No *interzooecial secondary tissue*.

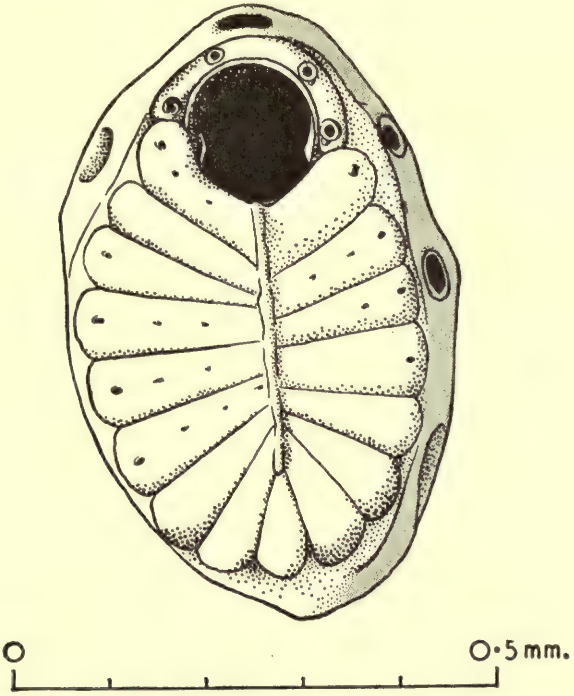


FIG. 49. *Leptocheilopora filliozati* (Brydone), D. 28294. Holotype of *L. arcuata* Lang. Adult zooecium with median ridge on frontal shield and large distal and lateral communication pores.

Avicularia apparently absent. *Ovicells* prominent, globular, but tending to be slightly pointed distally and flattened in front, hyperstomial, smooth, without *lateral slits*, and generally longer than wide. The lateral pair of oral spines may flank the entrance to the ovicell. *Young zooecia* and *ancestrulae* smaller than the adult zooecia, usually with 6 oral spines, and less often 5 or 4 in the slightly later stages of zoarial growth. There are generally fewer costae (8–12) than in the adult. The orifices, in the young stages, tend to have less marked proximal-lateral constrictions.

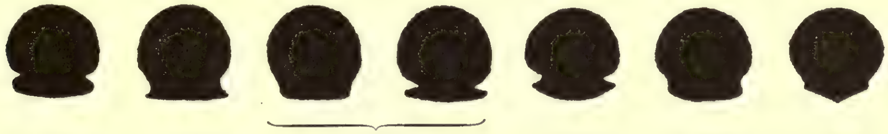
MEASUREMENTS. *Adult zooecia* Lz = 0·55 to 0·75 mm.
lz = 0·35 to 0·55 mm.
hr = 0·12 to 0·17 mm.
lr = 0·12 to 0·16 mm.
Young zooecia Lz = 0·33 to 0·54 mm.
lz = 0·22 to 0·37 mm.
hr = 0·09 to 0·15 mm.
lr = 0·08 to 0·13 mm.
Ancestrulae Lz = 0·28 to 0·36 mm.
lz = 0·17 to 0·25 mm.
hr = 0·09 to 0·10 mm.
lr = 0·07 to 0·10 mm.

REMARKS. *Leptocheilopora arcuata* Lang is a junior synonym of *L. filliozati* (Brydone). Of the specimens in the British museum (Natural History) collections available to Lang, he assigned only D.29900 to *L. filliozati* (Brydone). The specimen was presented in December, 1919 but was not mentioned by Lang in his 1921 catalogue. Measurement and comparison of this specimen with those assigned by Lang to *L. arcuata* suggested their synonymy, and this was confirmed by a detailed examination of Brydone's figured specimens of *L. filliozati*, S.M., B.36167–68. Among the nineteen zoaria examined, the adult zooecia of D.39425 and D.39432 were found to be slightly larger than normal and to possess slightly more costae (16–18). These specimens are therefore only tentatively referred to *L. filliozati* (Brydone).

It is of interest to note that the number of costae is not necessarily greater in more adult zooecia, but that occasionally the reverse may be true. For example, in the ancestrula of D.28894 there are apparently 12 costae, but the zooecia of the first growth ring, although larger, have only 9 or 10 costae each ; again, the largest zooecia of the holotype, and of paratypes D.4279, D.28893 and D.28895 have the fewest costae. The zooecium shown in Pl. 8, fig. 1 is distorted and of exceptional length (Lz = 1·30 mm., lz = 0·30 mm., hr = 0·16 mm., lr = 0·14 mm.), in this case there are 35 costae.

In *Leptocheilopora filliozati* (Brydone) Lz appears to vary less than lz, possibly because the width of a zooecium is more directly affected by restrictions imposed on it over a limited substratum. Apparently the development of the orifice is not usually restricted by normal growth conditions : thus, not only does hr slightly exceed lr, except in a very few instances where the two measurements are equal, but the maximum measurements also vary only a little and usually in proportion to one another. Even in the case of the abnormally long zooecium mentioned above the dimensions of the orifice are normal. The measurements of the orifice are therefore important diagnostically, although the orifices of zooecia of the same and of different zoaria may apparently vary in shape. This feature is illustrated by the following diagram (Text-fig. 50) of orifices from some of the specimens examined. Variation also occurs in the shape of the apertural bars. In both cases, some of the variation may be due to wear.

Leptocheilopora filliozati (Brydone) is smaller than *L. magna*, and lacks the constant form of the orifice of that species. It is easily distinguished from *L. tenuilabrosa* which has costate ovicells. The greater size and number of costae, and the fewer (4) oral spines in the adult zooecia of *L. filliozati* distinguish it from *L. vulnerata* (Brydone), which also has a different apertural bar and small lateral slits in the ovicell. *L. filliozati* is also characterized by the frequent development of an irregular median ridge on the frontal shield.



D.39429 D.39430 D.29900 D.39428 D.28294 D.39424

FIG. 50. *Leptocheilopora filliozati* (Brydone)—variation in the shape of the orifice.

STRATIGRAPHICAL DISTRIBUTION. Senonian, (? zone of *B. mucronata*), zones of *G.* [*A.*] *quadrata* and *O. pilula*, subzones of *E. scutata* var. *cincta* and *E. scutata* var. *depressula*.

SPECIMENS. D.28294. Holotype of *L. arcuata* Lang. Incomplete zoarium with ancestrula encrusting a fragment of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Cliffs between Rottingdean and Saltdean, east of Brighton, Sussex.

D.4279. Paratype of *L. arcuata* Lang. Zoarial fragment with ancestrula encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. East Harnham, south of Salisbury, Wiltshire. W. Gamble Collection.

D.4290. Paratype of *L. arcuata* Lang. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.4279.

D.4296. Paratype of *L. arcuata* Lang. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.4279.

D.28893–94. Two paratypes of *L. arcuata* Lang. Zoarial fragments encrusting pieces of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs between last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.

D.28895. Paratype of *L. arcuata* Lang. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit on East Hill, Rottingdean, east of Brighton, Sussex.

D.29900. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.28893–94.

D.39424, D.39426–28. Four zoarial fragments encrusting pieces of echinoid test (D.39424 with ancestrula). Senonian, zone of *G.* [*A.*] *quadrata*.

Pit 15 of Gaster, about one-third of a mile south-south-east of Salvington Windmill, and north of Hill Cottages, Salvington, Sussex.

?D.39425. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.39424.

D.39429. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 26 of Gaster, South Woodleighs Pit, east of gravel pit, north-east of Woodleighs Lodge, about half a mile west of Pit 24 of Gaster, Warningcamp, north-east of Arundel, Sussex.

D.39430. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.39424.

?D.39432. Incomplete zoarium encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Pit 8 of Rowe, south of Nodewell, Freshwater, Isle of Wight.

D.40932. Incomplete zoarium encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 87 of Gaster, near cart-track to Newlands Barn, north end of East Hill, Rottingdean, Sussex.

D.40933–35. Three incomplete zoaria encrusting fragments of echinoid test, the latter poorly preserved. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Section 113 of Gaster, cliffs between last groyne east of Rottingdean Gap and Saltdean, Sussex.

D.40936–38. Three incomplete zoaria encrusting fragments of echinoid tests. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 200 yards north of Trumley Copse, Lavant, Sussex.

D.40939. Incomplete zoarium encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Halnaker Chalk Pit, half a mile south of Halnaker Windmill, Boxgrove, Sussex.

OTHER MATERIAL. S.M., B.36167. Lectotype, labelled by Mr A. G. Brighton. "*Cribrilina filliozati* Brydone [Syntype]". See above.

S.M., B.36168. Zoarial fragment encrusting a piece of echinoid test. Labelled by Mr. A. G. Brighton "*Cribrilina filliozati* Brydone [Syntype]". Senonian, zone of *G.* [*A.*] *quadrata*. Locality 1054 of Brydone, Pit near a lane about one-eighth of a mile north-east of the Black Horse Inn, West Titherley, Hampshire. R. M. Brydone Collection.

4. ***Leptocheilopora vulnerata*** (Brydone)

(Pl. 9, figs. 1, 2; Text-fig. 51)

1914*b* *Cribrilina vulnerata* Brydone, p. 97, pl. 4, figs. 3, 4.
1916*a* *Leptocheilopora vulnerata* (Brydone) Lang, p. 396.
1921 *Leptocheilopora vulnerata* (Brydone): Lang, pp. xc, 70.

LECTOTYPE. (Chosen by Lang, 1921 : 70.) S.M., B.36271, the specimen figured by Brydone, 1914, pl. 4, fig. 3. Maastrichtian, zone of *Belemnella lanceolata* (*O. lunata* Chalk). Trimingham, Norfolk. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Leptocheilopora* with small zooecia (Lz = 0·42 to 0·50 mm., lz = 0·31 to 0·35 mm.) ; orifice small, of fairly constant size (hr = 0·10 to 0·12 mm., lr = 0·09 to 0·11 mm.) ; oral spines 7 ; costae 11–13, wide, distinct ; no intercostal spaces ; apertural bar triangular, produced slightly in the mid-line and sloping down to the proximal margin of the orifice ; ovicells smooth with small lateral slits.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* broadly oval, closely placed, with a single, large, oval *distal communication pore* and one or more smaller, oval *lateral communication pores*. *Orifice* small, distally and laterally rounded with a straight proximal margin ; slight proximal-lateral constrictions may be present. *Oral spines* 7, symmetrically and evenly spaced. *Frontal shield* flat or very gently arched, but descending steeply at the margins to meet the gymnocyst. *Costae* 11–13, wide, tapering inwards, distinct, closely placed. No *intercostal spaces* or *lateral costal fusions*. Three or four small *pelmata* with distinct, low rims occur on each costa ; they decrease in size inwards from the outer ends. *Apertural bar* triangular, with the apex pointing proximally and produced slightly in the mid-line : there is a prominent, curved facet on its descending distal side. *Gymnocyst* occasionally slightly exposed proximally to the frontal shield, but often obscured by the close placing of the zooecia.

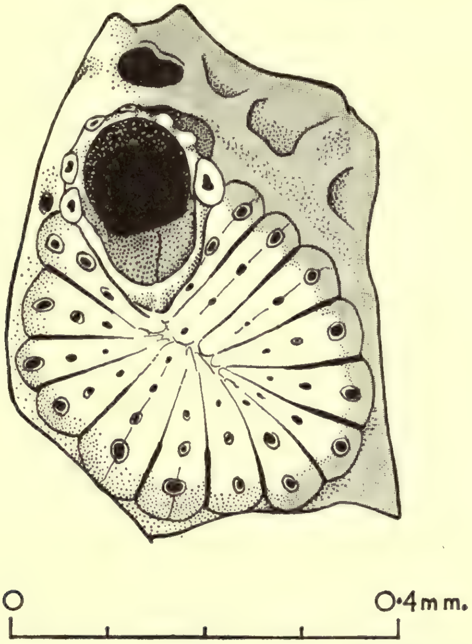


FIG. 51. *Leptocheilopora vulnerata* (Brydone), S.M., B.36271. Lectotype. Adult zooecium with seven oral spine-bases, prominent curved facet on apertural bar, distinctly rimmed small pelmata, and large distal—and smaller lateral—communication pores.

Avicularia apparently absent. *Ovicells* smooth, large, prominent, hyperstomial, globular, with small lateral slits. *Young zooecia* smaller than the adult zooecia, but otherwise similar, with 7 oral spines and 9–12 costae; the orifice is only slightly smaller than in the adult zooecia. *Ancestrula* very small, generally obscured.

MEASUREMENTS. *Adult zooecia* Lz = 0·42 to 0·50 mm.
lz = 0·31 to 0·35 mm.
hr = 0·10 to 0·12 mm.
lr = 0·09 to 0·11 mm.
Young zooecia Lz = 0·30 to 0·32 mm.
lz = 0·19 to 0·25 mm.
hr = 0·10 mm.
lr = 0·07 to 0·10 mm.
Ancestrula Not measurable.

REMARKS. *Leptocheilopora vulnerata* (Brydone) is distinguished from other species of the genus particularly by its small zooecial size, its constant number of oral spines, its relatively constant number of costae, and by the form of its apertural bar. The small lateral slits in the ovicell are also apparently peculiar to *L. vulnerata* (Brydone).

The lectotype, S.M., B.36271, and the other specimen originally figured by Brydone (1914*b*, pl. 4, fig. 4) S.M., B.36272, have been examined. Both are exceptionally well preserved and therefore retain very detailed characters such as the small, rimmed pelmata on the costae.

Lang (1921 : 70) doubted whether this species should be included in *Leptocheilopora*, but examination of Brydone's specimens shows that the species is accurately placed there and that Lang was mistaken in classifying the genus in the group of the cribrimorph Polyzoa lacking pelmata.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian, zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk) and ? upper part of zone of *B. mucronata*—Brydone (1914*b* : 97) stated " This species is abundant in the Trimingham Chalk and occurs sparingly in the Weybourne Chalk ".

MATERIAL. S.M., B.36271. Lectotype, labelled " *Cribrilina vulnerata* (Brydone) [Syntype] ". See above.

S.M., B.36272. Zoarium, with ancestrula, encrusting a piece of echinoid test. Labelled " *Cribrilina vulnerata* (Brydone) [Syntype] ". Horizon, locality and collection as for the lectotype.

?N.C.M.76.937 (28/1). Zoarial fragment with young zooecia encrusting a test of *Cardiaster ananchytis* (Leske). Senonian, zone of *B. mucronata*. Thorpe St. Andrews, Norwich, Norfolk. R. M. Brydone Collection.

SPECIES OF UNCERTAIN SYSTEMATIC POSITION PREVIOUSLY ASSIGNED TO *LEPTOCHEILOPORA*

(1) ***Leptocheilopora longuessensis*** Lang.

1916*a* *Leptocheilopora languessensis* [*sic*] Lang, pp. 396, 397.

See remarks under *Leptocheilopora magna* Lang (p. 106).

(2) *Reptoporella regularis* d'Orbigny.

1852 *Reptoporella regularis* d'Orbigny, p. 717, figs. 6, 7.
1853 *Reptoporella regularis* d'Orbigny : d'Orbigny, p. 475.
1854 *Reptoporella regularis* d'Orbigny : d'Orbigny, p. 1097.

REMARKS. Lang (1916*a* : 397 ; 1921 : 70) tentatively referred *Reptoporella regularis* d'Orbigny to *Leptocheilopora*. However, the placing of d'Orbigny's species cannot be at all certain without actual material being examined. The figures show a cribrimorph polyzoan with prominent hyperstomial ovicells and distal to each a smaller round structure with a median proximal pore. Lang (1916*a*) regarded this as the distal communication pore, but this is usually only visible at the edges of a zoarium where the distal walls of the zooecia may be clearly exposed. The structure might even be avicularian. As Lang stated (1921 : 71), " The structure and systematic position of the species, . . . as of the genus *Reptoporella* of which *R. regularis* is the genotype, remains conjectural ".

I do not agree that *Membranipora crenulata* d'Orbigny (1852, pl. 728, figs. 13–15 ; 1853 : 547 ; 1854 : 1093) is, as suggested by Canu (1900*b* : 449) synonymous with *Reptoporella regularis* d'Orbigny. Gillard (1943 : 186) also disagreed with Canu on this point, and stated " la figure de d'Orbigny à été exagérément retouchée au point de prêter aux plus graves confusions. Les septules distales ont été reproduites à l'éxtrémité de chaque zoécie, si bien que Canu a pu supposer que chaque lignée zoéciale débutait par un avicellaire intercalé."

Evidently Gillard assigned several specimens, from the Upper Campanian of the Royan area, to *Leptocheilopora regularis* (d'Orbigny) as he also stated (1943 : 186), " Plusieurs zoaria recueillis à Port-Marant et à la base de la falaise E. de Talmont, se rapportent à cette espèce dont les zoécies montrent des traces d'épines aréales très ténues. Lz = 700–800 μ, lz = 350–375 μ, La [=hr] = 80 μ, la [= lr] = 100 u."

Genus *PELMATOPORA* Lang

1851 *Escharipora* d'Orbigny, pls. 603, 684–687, 700, 703 [*partim*].
1852 *Escharipora* : d'Orbigny, p. 221 [*partim*].
1852 *Semiescharipora* d'Orbigny, pls. 717–719 [*partim*].
1853 *Semiescharipora* : d'Orbigny, p. 479 [*partim*].
1854 *Escharipora* : d'Orbigny, p. 1097 [*partim*].
1854 *Semiescharipora* : d'Orbigny, p. 1097 [*partim*].
1860 *Escharipora* : Coquand, p. 121.
1860 *Semiescharipora* : Coquand, p. 150.
1885 *Semiescharipora* : Vine, pp. 116, 156.
?1889*a* *Cribrilina* : Pergens, pp. 61, 69.
1893 *Cribrilina* : Pergens, pp. 202, 216.
1893 *Cribrilina* : Vine, pp. 316, 323, 336.
1900*a* *Cribrilina* : Canu, p. 409.
1900*b* *Cribrilina* : Canu, p. 445 [*partim*].
1900*b* *Escharipora* : Canu, p. 457 [*partim*].
1900 *Cribrilina* : Rowe, p. 341.
1904 *Cribrilina* : Jukes-Browne, p. 490.
1906 *Cribrilina* : Brydone, p. 300.
1910 *Cribrilina* : White, pp. 55, 56.

1911 *Cribrilina* : Canu, pp. 252 [*partim*], 280.
1912 *Cribrilina* : White, pp. 35, 43.
1912 *Cribrilina* : Brydone, pp. 20, 53, 70–89, 95.
1913 *Cribrilina* : Brydone, p. 436 [*partim*].
?1913 *Cribrilina* : White, pp. 24, 27, 30, 32, 38 [*partim*].
1913 *Cribrilina* : Lang, p. 171.
1916*a* *Carydiopora* Lang, p. 94 [*partim*].
1916*a* *Pelmatopora* Lang, p. 101.
1917 *Cribrilina* : Brydone, p. 495.
1919*c* *Pelmatopora* : Lang, p. 107.
1919*d* *Pelmatopora* : Lang, pp. 191, 197, 204, 210.
1921 *Pelmatopora* : Lang, pp xcvi–xcv.
1921 *Cribrilina* : Lang, p. lvii [*partim*].
1922 *Pelmatopora* : Lang, p. 240.
?1923 *Cribrilina* : Waters, p. 546 [*partim*].
1923 *Pelmatopora* : Waters, p. 555.
?1924 *Cribrillina* [*sic*] : Böhm, p. 101.
1924 *Pelmatopora* : Gaster, second of three tables opp. p. 110.
1924*c* *Pelmatopora* : Voigt, p. 110.
?1924*d* *Cribrilina* : Voigt, p. 236 [*partim*].
1924 *Cribrilina* : White, pp. 55, 62.
?1925*a* *Cribrilina* : Voigt, p. 25 [*partim*].
?1925*b* *non Pelmatopora* : Voigt, pp. 98–102.
1927 *Pelmatopora* : Canu & Bassler, pp. 18, 35.
1930 *Pelmatopora* : Gaster, table opp. p. 340.
1930 *non Pelmatopora* : Voigt, pp. 515, 544, 561.
1935 *Pelmatopora* : Bassler, pp. 31, 165.
1939 *non Pelmatopora* : Voigt, p. 93.
1942 *Pelmatopora* : Gillard, p. 90.
1953 *Pelmatopora* : Bassler, p. G192.
1958 *Pelmatopora* : Didon, pp. 80, 82–85.

TYPE SPECIES. *Pelmatopora pero* Lang, 1916*a* : 101. Senonian, top of zone of *M. cor-anguinum*. Medical College Pit, Epsom, Surrey. F. Möckler Collection.

EMENDED DIAGNOSIS. Pelmatoporinae with or without a secondary orifice—where present it comprises a distal oral shield of secondary tissue tending to envelope the unmodified oral spines, or the oral shield may be partly formed by a pair, occasionally two pairs, of enlarged oral spines ; apertural bar lacking a median process ; avicularia variable, relatively small, rounded, sporadically distributed in the species in which the distal oral shield is not developed, but commonly paired near the orifice, large, distally pointed and directed in the species with distal oral shields.

REMARKS. All the material originally assigned to *Pelmatopora* by Lang has been re-examined. Similarly, all the specimens figured by Brydone which Lang regarded as *Pelmatopora* species have been examined. In addition a large number of specimens, particularly from the upper zones of the Senonian, in the C. T. A. Gaster Collection, have been incorporated in the revision.

Lang (1922 : 241), in his remarks on *Pelmatopora*, was concerned primarily with tracing the stratigraphical relationships of the species which he recognized. The present revision shows that several of the species which he described are synonymous, and that their stratigraphical relationships are, in some cases, different from those on which Lang based some of his evolutionary theory.

Lang (1916*a* : 102 ; 1922 : 251) originally distinguished 38 species of *Pelmatopora*. Voigt (1925*b* : 99, 100 ; 1930 : 514) subsequently described two more. Voigt's species are here not definitely assigned to *Pelmatopora* (see p. 200), and only 22 of the species recognized by Lang are maintained here. It has not proved necessary to establish any new species of *Pelmatopora*.

The revision is summarized by the following comparative list of Lang's and present identifications. Only those specimens probably available to Lang when he prepared volume 4 of the *Catalogue of Cretaceous Bryozoa* (1922) are considered. The species are listed in the same order as that used by Lang in 1922.

Lang's identifications (1922)	Present identifications
1. *P. calceata*, Lang	*P. calceata* Lang, p. 123.
2. *P. crepidaria* Lang	*P. crepidaria* Lang, p. 125.
3. *P. solearis* Lang	*P. solearis* Lang, p. 127.
4. *P. larva*, sp. n.	*P. larva* Lang, p. 134 ; and *P. d'orbignyi* Lang [*partim*], p. 140.
5. *P. chrysalis* (d'Orbigny)	*P. chrysalis* (d'Orbigny), p. 132 ; and *P. larva* Lang [*partim*], p. 134.
6. *P. striata* (d'Orbigny)	*P. striata* (d'Orbigny), p. 136.
7. *P. d'orbignyi* Lang	*P. d'orbignyi* Lang, p. 140.
8. *P. pauciclavia* Lang	*P. fragilis* (d'Orbigny), p. 138.
9. *P. fragilis* (d'Orbigny)	*P. fragilis* (d'Orbigny), p. 138.
10. *P. quadrata* Lang	*P. quadrata* Lang, p. 143.
11. *P. filliozati* Lang	*P. quadrata* Lang, p. 143.
12. *P. insignis* (Canu)	? *P. suffulta* (Brydone), p. 151.
13. *P. suffulta* (Brydone)	*P. suffulta* (Brydone), p. 151.
14. *P. gasteri* Lang	*P. gasteri* Lang, p. 130.
15. *P. repleta* (Brydone)	*P. suffulta* (Brydone), p. 151.
16. *P. interrupta* (d'Orbigny)	*P. chrysalis* (d'Orbigny), p. 132 ; and *P. larva* Lang, p. 134.
17. *P. simplex* Lang	*P. simplex* Lang, p. 157.
18. *P. coryli* Lang	*P. coryli* Lang, p. 168.
19. *P. fecampensis* Lang	*P. fecampensis* Lang, p. 145.
20. *P. plantaris* Lang	*P. plantaris* Lang, p. 159.
21. *P. pero* Lang	*P. pero* Lang, p. 148 ; and *P. brydonei* Lang [*partim*], p. 164.
22. *P. brydonei* Lang	*P. brydonei* Lang, p. 164.
23. *P. quadrivolucris* Lang	*P. quadrivolucris* Lang, p. 161.
24. *P. marsupitum* [*sic*] Lang	*P. marsupitorum* Lang, p. 171.
25. *P. roedeanensis* Lang	*P. marsupitorum* Lang, p. 171.
26. *P. somptingensis* Lang	*P. somptingensis* Lang, p. 188.
27. *P. gregoryi* (Brydone)	*P. gregoryi* (Brydone), p. 175 ; and *P. palmata* Lang [*partim*], p. 196.
28. *P. palmata* Lang	*P. palmata* Lang, p. 196.
29. *P. damicornis* Lang	*P. palmata* Lang, p. 196.
30. *P. danktonensis* Lang	*P. somptingensis* Lang, p. 188.
31. *P. bidens* Lang	*P. gregoryi* (Brydone), p. 175.
32. *P. lancingensis* Lang	*P. gregoryi* (Brydone), p. 175.
33. *P. saltdeanensis* Lang	*P. gregoryi* (Brydone), p. 175.

34. *P. collium* Lang . . . . . *P. gregoryi* (Brydone), p. 175.
35. *P. promontoriorum* Lang . . . . *P. gregoryi* (Brydone), p. 175.
36. *P. ranunculoides* Lang . . . . *P. gregoryi* (Brydone), p. 175.
37. *P. lacuum* Lang . . . . . *P. gregoryi* (Brydone), p. 175.
38. *P. gyrinoides* Lang . . . . . *P. gregoryi* (Brydone), p. 175.

Pelmatopora is distinguished from other genera of the Pelmatoporinae by the type of avicularia which are commonly present, and particularly by the absence of prominent distal or proximal oral shields.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *M. cortestudinarium* to *G.* [*A.*] *quadrata*, ?zone of *B. mucronata* and ?Danian.

KEY TO THE SPECIES OF *PELMATOPORA* LANG

(I) *Pelmatopora* with unmodified oral spines.

(A) Median area of fusion narrow; frontal shield arched; orifice often with proximal-lateral constrictions; no lateral costal fusions; gymnocyst well exposed; large pelmata only.

(1) Interzooecial secondary tissue entirely absent; avicularia small, rounded, sporadic . . . . 1. ***P. calceata*** Lang

(2) Interzooecial secondary tissue present.

(*a*) Interzooecial secondary tissue only slightly developed; avicularia small, rounded, tubular, in two pairs near the orifice 2. ***P. crepidaria*** Lang

(*b*) Interzooecial secondary tissue abundant; avicularia small, rounded, one pair near orifice . . . . 3. ***P. solearis*** Lang

(B) Median area of fusion wider.

(1) Orifice small (hr = lr), with marked proximal-lateral constrictions; lateral costal fusions present . . . . 4. ***P. gasteri*** Lang

(2) Orifice without marked proximal-lateral constrictions.

(*a*) Lateral costal fusions absent; interzooecial secondary tissue abundant with marked lacunae; gymnocyst concealed.

(i) Large pelmata only; frontal shield flat.

(*a'*) Orifice higher than wide; avicularia small, rounded, sporadic 5. ***P. chrysalis*** (d'Orbigny)

(*b'*) Orifice wider than higher.

(*a''*) Avicularia large, pointed . . . 6. ***P. larva*** Lang

(*b''*) Avicularia small, rounded, sporadic, occasionally tending to be paired; 25 or more costae 7. ***P. striata*** (d'Orbigny)

(ii) Pelmata and pelmatidia present; frontal shield arched; 10–15 costae . . . . 8. ***P. fragilis*** (d'Orbigny)

(*b*) Lateral costal fusions present; interzooecial secondary tissue abundant.

(i) Orifice higher than wide; frontal shield flat; avicularia relatively large, pointed, paired . . . . . 9. ***P. d'orbignyi*** Lang

(ii) Orifice wider than high.

(*a'*) Avicularia large, pointed, paired.

(*a''*) Frontal shield arched . . . 10. ***P. quadrata*** Lang

(*b''*) Frontal shield relatively flat.

(*a'''*) Aperturai bar wide with slight median furrow; zooecia small, costae well spaced 11. ***P. fecampensis*** Lang (*b'''*) Apertural bar narrow with slight median ridge; zooecia large; costae closely placed; pematidia occasionally present . . . 12. ***P. pero*** Lang

(*b'*) Avicularia small, rounded, paired.

(*a''*) Pelmata and pelmatidia present; 15–20 costae; large zooecia; amount of interzooecial secondary tissue variable but never markedly developed 13. ***P. suffulta*** (Brydone)

(*b''*) Pelmatidia more numerous; Lz less than 1·00 mm.; interzooecial secondary tissue markedly developed with conspicuous lacunae.

(*a'''*) Costae narrow, 16–18 . . 14. ***P. simplex*** Lang

(*b'''*) Costae wide, 13–16 . . 15. ***P. plantaris*** Lang

(II) *Pelmatopora* with enlarged oral spines.

(A) Two pairs of enlarged oral spines present . . 16. ***P. quadrivolucris*** Lang

(B) Only the distal pair of oral spines enlarged.

(1) Proximal pair of unmodified oral spine bases often still visible 17. ***P. brydonei*** Lang

(2) Unmodified oral spines entirely obscured by secondary tissue accumulated round the margin of the orifice (may be visible in early growth stages).

(*a*) Avicularia small, rounded, occasional, sporadic; zooecia small; 11–14 costae. . . . . 18. ***P. coryli*** Lang

(*b*) Avicularia large, distally pointed and directed usually paired.

(i) Enlarged distal oral spines relatively short and peg-like; 14–20 costae . . . . 19. ***P. marsupitorum*** Lang

(ii) Enlarged distal oral spines elongate, pointed, relatively slender, with a strong tendency to bifurcate—the outer horn of the bifurcation curving away laterally and proximally . 20. ***P. gregoryi*** (Brydone)

(iii) Enlarged distal oral spines laterally flattened and distally expanded, with a marked tendency to bifurcate . 21. ***P. somptingensis*** Lang

(iv) Enlarged distal oral spines very broad distally and distinctly bilobed . . . . . . 22. ***P. palmata*** Lang

The following species are omitted from the above key and are regarded as of uncertain systematic position: *Pelmatopora incerta* Voigt (1925*b* : 99, 100), *P. grandiporosa* Voigt (1930 : 514), *Pelmatopora* sp. Voigt (1930 : 514), *Pelmatopora daniensis* Voigt (1925*b* : 99, 100). They are discussed on p. 200.

1. ***Pelmatopora calceata*** Lang

(Pl. 9, fig. 3; Text-fig. 52)

1916*a* *Pelmatopora calceata* Lang, p. 102.
1919*d* *Pelmatopora calceata* Lang: Lang, pp. 191, 196, 210, 218, 223, text-figs. 1, 49.
1921 *Pelmatopora calceata* Lang: Lang, p. xciv.
1922 *Pelmatopora calceata* Lang: Lang, p. 254, pl. 5, fig. 6; text-fig. 74.

HOLOTYPE. D.4032. Well preserved zoarial fragment encrusting a piece of echinoid test. Senonian, either base of zone of *M. cor-anguinum* or top of zone of *M. cortestudinarium*. Chatham, Kent. W. Gamble Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with no distal oral shield; oral spine bases unmodified, in two pairs; median area of fusion narrow; pelmata present but no pelmatidia ; frontal shield strongly arched ; no interzooecial secondary tissue ; avicularia small, apparently rounded, sporadic.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Zooecia* broadly oval, small. *Orifice* evenly rounded distally, the sides and proximal margin straight, occasionally with proximal-lateral constrictions, the rim not secondarily thickened. *Oral spine bases* 4, not enlarged, unmodified, the proximal-lateral pair placed on the distal-lateral curves of the orifice and not indenting its outline. *Frontal shield* strongly arched. *Costae* 10–14, widely spaced at the outer ends, with no *lateral costal fusions*. Each costa bears a prominent, large *pelma* near its inner end. The outlines of the inner ends of individual costae may be traced in the narrow *median area of fusion*. *Apertural bar* straight, slightly thickened, with two prominent pelmata near the mid-line ; no *median process*. *Gymnocyst* well exposed laterally and particularly proximally to the frontal shield. No *interzooecial secondary tissue*.

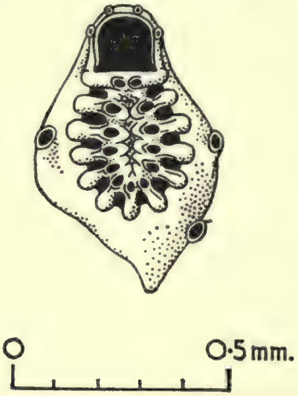


FIG. 52. *Pelmatopora calceata* Lang, D.4032. Holotype. Adult zooecium and three small, oval, sporadic avicularia.

Avicularia numerous, probably variously directed, sporadic, small, rounded, possibly adventitious on the sides of the zooecia rather than interzooecial, though this is not certain. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·54 to 0·75 mm.
lz = 0·33 to 0·39 mm.
hr = 0·12 mm.
lr = 0·12 mm.
Avicularia Not measurable.

REMARKS. The only available specimen of *P. calceata*, the holotype, has been re-examined. Lang slightly underestimated the dimensions, those of the orifice are particularly constant. The range in number of costae is 10–14 and not 14–16 as stated (Lang, 1922 : 254). The avicularia are very small and it is not possible to determine whether they are proximally or distally directed ; there is a slight suggestion of proximal-lateral constrictions in some avicularian apertures, possibly indicating distally directed rostra which are larger than the proximal portions of the apertures. Lang regarded this species as a radical form.

Stratigraphical distribution. Senonian, either base of zone of *M. cor-anguinum* or top of zone of *M. cortestudinarium*.

Specimen. D.4032. Holotype—see above.

2. ***Pelmatopora crepidaria*** Lang

(Pl. 9, fig. 4 ; Text-figs. 53, 54)

1916*a* *Pelmatopora crepidaria* Lang, p. 102.
1919*d* *Pelmatopora crepidaria* Lang : Lang, pp. 211, 222, 224, text-fig. 47.
1921 *Pelmatopora crepidaria* Lang : Lang, p. xciv.
1922 *Pelmatopora crepidaria* Lang : Lang, p. 255, pl. 5, fig. 7 ; text-fig. 75.

Holotype. D.21200. Well-preserved zoarial fragment. Senonian, zone of *M. cor-anguinum*. Woburn Green, south-west of Beaconsfield, Buckinghamshire. L. Treacher Collection.

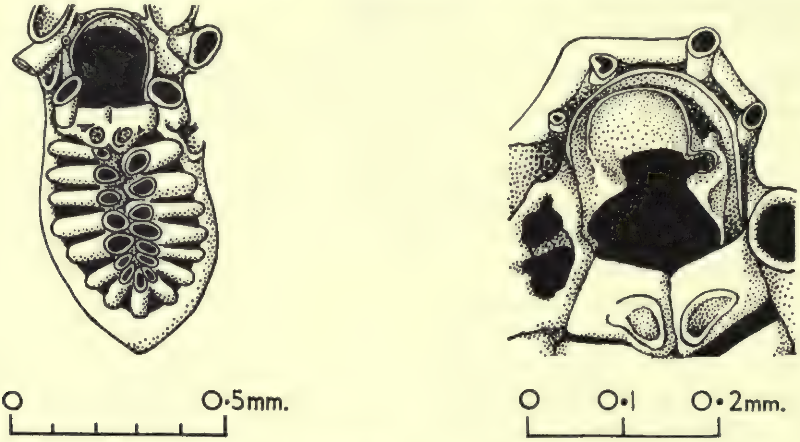
Emended diagnosis. *Pelmatopora* with unmodified oral spine-bases ; no pelmatidia ; frontal shield very well arched ; interzooecial secondary tissue irregularly developed in small amounts particularly near the orifices ; avicularia small, rounded, prominent, tubular, occurring in one or two pairs near the orifice.

Description. *Zoarium* unilaminar, probably always encrusting. *Zooecia* somewhat elongate, oval. *Orifice* of equal height and width, large, evenly rounded distally and laterally with slight proximal-lateral constrictions and a straight proximal margin ; the outline of the orifice is not obscured by the accumulation of secondary calcareous tissue. *Oral spine-bases* 4, in two pairs, widely placed, well developed, but unmodified and not enlarged, not indenting the outline of the orifice. Secondary closure of the orifice may occur, as in the holotype. An irregular, curved, calcareous shelf may be formed deep in the distal half of the orifice and extend proximally along the lateral margins. In other zooecia the orifice may be completely closed by an irregular lamina of secondary calcareous tissue, see Pl. 9, fig. 4 and Text-fig. 54. *Frontal shield* well arched, elongate. *Costae* 11–14, closely spaced ; no *lateral costal fusions*. Each costa bears a large *pelma* very close to its inner end. *Median area of fusion* narrow. *Apertural bar* prominent, very wide, thickened, with a very slight median ridge and two prominent, large pelmata, one on either side of and close to the mid-line ; no *median process* developed. *Gymnocyst* smooth, somewhat obscured by the irregular, small amounts of *interzooecial secondary tissue* which are developed particularly near the orifices. The gymnocyst is usually exposed laterally and especially proximally to the frontal shields. The interzooecial valleys are deep and sharply defined.

Avicularia very prominent but small, apparently directed distally and obliquely outwards from the zooecia they accompany, rounded and raised on elongate, stout, tubular stalks which project above the general level of the arched frontal shields. The avicularia are usually arranged in a proximal-lateral and a distal-lateral pair near the margins of the orifice : but proximal-lateral pairs occur more frequently than distal-lateral pairs. Other similar, sporadic avicularia are occasionally present. *Ovicells* not seen.

MEASUREMENTS. Zooecia Lz = 0·66 to 0·81 mm.
lz = 0·35 to 0·39 mm.
hr = 0·15 to 0·18 mm.
lr = 0·15 to 0·18 mm.
Avicularia Not measurable.

REMARKS. The holotype, D.21200, and the paratype, D.4110, have been re-examined. The former is a very well preserved zoarial fragment which is now unattached, the latter is a worn zoarial fragment encrusting a piece of echinoid test.



FIGS. 53, 54. *Pelmatopora crepidaria* Lang, D.21200. Holotype.

(53) Adult zooecium with two pairs of tubular avicularia near the orifice.

(54) Distal part of adult zooecium, the tubular avicularia abraded and an irregular calcareous lamina developed in the distal and distal-lateral parts of the orifice.

Lang's measurements for the species are, apparently, maximum dimensions; generally the zooecia are smaller, usually about 0·35 mm. wide and about twice as long. The range in number of costae is 11–14, but usually less than 14. It is not possible to determine whether all the avicularia are distally directed outwards from the zooecia they accompany. The avicularia project and are thus often worn at their upper ends.

Compared with the zooecia of *P. calceata* those of *P. crepidaria* are more closely spaced, their median areas of fusion are not so wide, their costae have less rounded outer ends, and their intercostal spaces are narrower and longer.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum*.

SPECIMENS. D.21200. Holotype—see above.

D.4110. Paratype. Worn zoarial fragment encrusting a piece of echinoid test. Senonian, (zone unspecified). Chatham, Kent. W. Gamble Collection.

3. *Pelmatopora solearis* Lang

(Pl. 9, figs. 5, 6 ; Text-figs. 55, 56)

1916*a*	*Pelmatopora solearis* Lang, p. 102.
1919*d*	*Pelmatopora solearis* Lang : Lang, pp. 210, 213, 218, 223, text-fig. 50.
1921	*Pelmatopora solearis* Lang : Lang, pp. xciv, xcv.
1922	*Pelmatopora solearis* Lang : Lang, p. 257, pl. 5, fig. 8 ; text-fig. 76.
1930	*Pelmatopora solearis* Lang : Gaster, table opp. p. 340.

HOLOTYPE. D.21211. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*. Hurley Bottom, Berkshire, south-east of Henley, Oxfordshire. L. Treacher Collection.

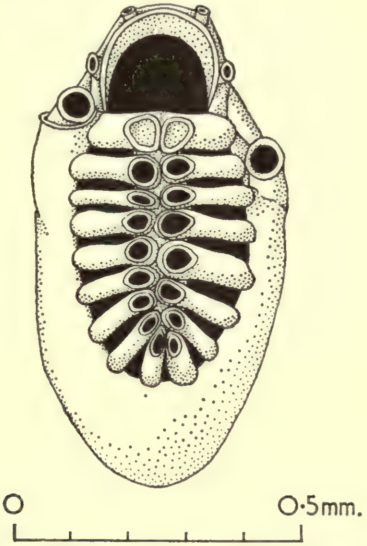


FIG. 55. *Pelmatopora solearis* Lang, D. 2763. Paratype. Adult zooecium and two worn avicularia ; there is no interzooecial secondary tissue round the zooecium.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; median area of fusion may be narrow or wide ; no well-developed pelmatidia ; interzooecial secondary tissue relatively abundant ; avicularia small, rounded, sporadic, tending to be paired, one near each proximal-lateral corner of the orifice.

DESCRIPTION. *Zoarium* unilaminar, probably always encrusting. *Adult zooecia* broadly oval, often nearly parallel-sided and elongate. *Orifice* generally a little wider than high, evenly rounded distally, with straight sides and a straight proximal margin. Occasionally very slight proximal-lateral constrictions occur. The outline of the orifice is not obscured by the accretion of secondary calcareous tissue. *Oral spine-bases* 4, unmodified, the lateral pair tending to be larger than the distal pair, but not indenting the outline of the orifice. *Frontal shield* well arched, but often flat in the median area. *Costae* 14-24, usually 14–19, fairly closely spaced with no *lateral costal fusions*. Each costa bears a large *pelma* very close to its inner end.

Very occasionally a small *pelmatidium* may also occur. The pelmata often form a prominent " rim " to the *median area of fusion* which may be narrow and elongate, with the double row of large pelmata lying close together, or it may be wide, with the two rows of pelmata further away from the mid-line of the frontal shield. When the median area of fusion is wide the outlines of the inner ends of individual costae may be traced across it. *Apertural bar* straight and somewhat triangular, prominent, wide, rounded on its upper surface and thickened, with two large, but shallow, pelmata, one on either side of, and close to, the mid-line; no *median process*.

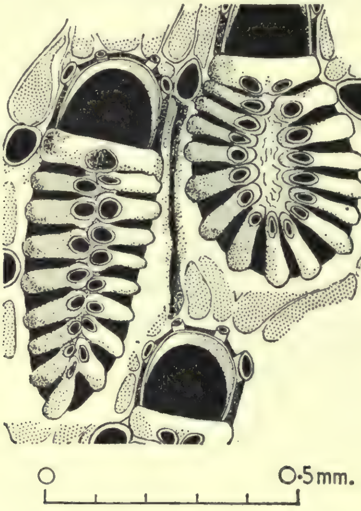


FIG. 56. *Pelmatopora solearis* Lang, D.19510. Paratype. Two adult zooecia and orifice of a proximally adjacent third zooecium and five worn avicularia. The contour-like development of interzooecial secondary tissue is apparent. The frontal shield of the zooecium on the right has a wide median area of fusion, contrasting with that of the zooecium on the left where the pelmata are close to the mid-line.

Gymnocyst smooth, often well exposed, particularly proximally to the frontal shield, but it may be considerably, and even completely, obscured by *interzooecial secondary tissue* accumulated in contour-like ridges and eventually filling the interzooecial furrows. Irregular *lacunae* occur in this secondary tissue.

Avicularia numerous, small, oval to rounded, occasionally somewhat pointed distally, sporadic, or tending to occur in pairs, one avicularium occurring near each proximal-lateral corner of the orifice. *Ovicells* not seen. *Young zooecia* smaller than the adult zooecia. Orifice of the same size and shape as in the adult zooecia. Oral spine-bases 4. Frontal shield more arched than in the adult stages, with about 12 costae. Each costa has a large pelma at its inner end close to the mid-line, the median area of fusion always being very narrow. The apertural bar is stout with two prominent pelmata near the mid-line, and the gymnocyst is well exposed. Interzooecial secondary tissue is scanty or absent in the young stages. The avicularia are small, rounded and generally sporadic, but tend to occur in the paired arrangement found more commonly in the adult stages.

MEASUREMENTS. *Adult zooecia* Lz = 0·63 to 1·00 mm.
lz = 0·32 to 0·50 mm.
hr = 0·12 to 0·18 mm.
lr = 0·12 to 0·21 mm.
Young zooecia Lz = 0·50 mm.
lz = 0·30 mm.
hr = 0·12 to 0·15 mm.
lr = 0·15 to 0·18 mm.
Avicularia Not measurable.

REMARKS. Lang's description was based mainly on the holotype. This, with all paratypes, has been re-examined, as well as several other specimens. In the many zooecia measured, costae were found to be more numerous in the larger than in the smaller ones. D.2813 possesses one abnormally long zooecium (Lz = 1·45 mm., lz = 0·33 mm.) with about 35 costae. The most variable feature is the amount of interzooecial secondary tissue which may be developed. It may be absent or very abundant in different specimens, and occasionally varies from scarce to abundant in the same zoarium. As Lang has suggested, the young zooecia of *P. solearis* are similar to the adult zooecia of *P. calceata*, the radical form, according to Lang, from which *P. solearis* may be derived. Most of the specimens assigned by Lang to *P. solearis* encrust fragments of echinoid test. D.24542, D.27043–46, D.28265 and D.4221 are now unattached.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *M. cortestudinarium* and *M. cor-anguinum.*

SPECIMENS. D.21211. Holotype—see above.

D.28267. Paratype. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum, Trochiliopora* Bed (about 20 ft. above base of zone). Hindover, north-east of Seaford, Sussex.

D.28268. Paratype. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum, Trochiliopora* Bed. Cliff End, east side of Cuckmere Haven, Sussex.

D.24542. Paratype. Zoarial fragment, now unattached. Senonian, zone of *M. cor-anguinum.* Gillingham, north-east of Chatham, Kent. W. Gamble Collection.

D.27042–46. Paratypes. Five fragments of the same unattached zoarium. Senonian, zone of *M. cortestudinarium.* Lower pit, Slines Oak, Worms Heath, Warlingham, Surrey. F. Möckler Collection.

D.19510. Paratype. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cortestudinarium.* Seaford, Sussex. F. Möckler Collection.

D.28269. Paratype. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cortestudinarium.* Cliffs between Hope Gap and Cuckmere Haven, Sussex.

D.2763, D.2813, D.2817, D.27980. Four paratypes. Zoarial fragments now unattached. Senonian, either base of zone of *M. cor-anguinum* or top of zone of *M. cortestudinarium*. Chatham, Kent. G. R. Vine Collection.

D.4026, D. 4971, D.4978. Three paratypes. Zoarial fragments, now unattached. Horizon and locality as for D.2763. W. Gamble Collection.

D.4030, D.4221, D.4965. Three poorly preserved zoarial fragments, now unattached. Horizon and locality as for D.2763. W. Gamble Collection.

D.28265–66. Two zoarial fragments, the former now unattached, the latter encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed, Summit of the Downs, Mount Harry, near Lewes, Sussex.

D.40134. Zoarial fragment encrusting a piece of echinoid test. Lower Senonian, zone unspecified. ?Chatham, Kent. W. Gamble Collection.

D.40135. Zoarial fragment encrusting a piece of echinoid test. Lower Senonian, zone unspecified. ?Chatham, Kent. Collection unspecified.

D.40722–27. Six unattached zoarial fragments. Horizon, locality and collection as for D.28265—see above.

D.40728–31. Four unattached zoarial fragments. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed. Cliffs, Beltout, west of Eastbourne, Sussex.

D.40732–33. Two unattached zoarial fragments. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed. Cliffs, east side of Cuckmere Haven, east of Seaford, Sussex.

D.40734–35. Two zoarial fragments encrusting pieces of echinoid tests. Senonian, zone of *M. cortestudinarium*. Cliffs between Hope Gap and Cuckmere Haven, east of Seaford, Sussex.

4. ***Pelmatopora gasteri*** Lang

(Pl. 9, fig. 8 ; Text-fig. 57)

1916*a* *Pelmatopora gasteri* Lang, pp. 102, 105.
1919*d* *Pelmatopora gasteri* Lang : Lang, pp. 211, 218, 222, 226, text-fig. 44.
1921 *Pelmatopora gasteri* Lang : Lang, p. cxiv.
1922 *Pelmatopora gasteri* Lang : Lang, p. 278, pl. 5, fig. 12 ; text-fig. 84.

HOLOTYPE. D.28274. The only specimen. Fragment of a well-preserved zoarium, now unattached. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed, about 20 ft. above base of zone. Cliffs, east side of Cuckmere Haven, Sussex.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; pelmatidia present ; avicularia tend to be paired but are occasionally sporadic ; costae 15–17 ; zooecia small (Lz = 0·60 to 0·72 mm., lz = 0·33 to 0·36 mm.) ; orifice with marked proximal-lateral constrictions.

DESCRIPTION. *Zoarium* unilaminar, now unattached. *Zooecia* oval, small. *Orifice* of equal height and width, rounded distally and laterally, with a straight proximal margin and with marked proximal-lateral constrictions. *Oral spine-bases* unmodified, occurring in two pairs, the proximal-lateral pair slightly larger. The outline of the orifice may be very slightly indented by the oral spine bases. *Frontal shield* steeply arched, but with a flat median area of fusion. *Costae* 15–17, each with a fairly prominent *pelma* near its inner end, and, closer to the mid-line of the frontal shield, often with an obscure *pelmatidium*. *Lateral costal fusions* occur at the level of the pelmata only. *Median area of fusion* fairly narrow, spindle-shaped. *Apertural bar* prominent, flat, very wide, with two pelmata, one on each side of and close to the mid-line. *Gymnocyst* obscured by *interzooecial secondary tissue*, which, though abundant, does not encroach on to the frontal shields. Slight, irregularly elongate depressions are present in the interzooecial secondary tissue.

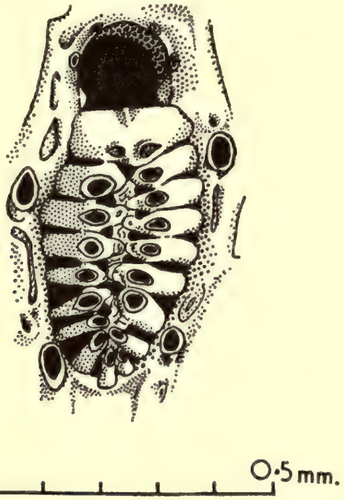


FIG. 57. *Pelmatopora gasteri* Lang, D.28274. Holotype. Adult zooecium and paired, worn avicularia. The two avicularia at the proximal end belong to adjacent zooecia.

Avicularia tend to occur just proximally to the proximal-lateral corners of the orifice, often paired. Other occasional, sporadic, interzooecial avicularia occur. All are small, elongate-oval and probably distally directed. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·60 to 0·72 mm.
lz = 0·33 to 0·36 mm.
hr = 0·12 mm.
lr = 0·12 mm.
Avicularia Not measurable.

REMARKS. The unique holotype has been re-examined. The oral spine-bases are larger than is suggested by Lang's figure (1922, text-fig. 84), and the avicularia tend to be paired rather than sporadic. The pelmatidia lie very close to the mid-line in the median area of fusion and are generally obscured by slight extra-calcification or by wear along the mid-line. The form and constant small size of the orifice, the relatively small zooecia, and the restricted range in number of costae particularly distinguish this species. No other specimens have been found in the large amount of material examined from the C. T. A. Gaster Collection.

Stratigraphical distribution. Senonian, zone of *M. cor-anguinum*.

Specimen. D.28274. Holotype—see above.

5. *Pelmatopora chrysalis* (d'Orbigny)

(Pl. 9, fig. 7; Text-fig. 58)

1851 *Escharipora chrysalis* d'Orbigny, pl. 686, figs. 6–8 (as *chrisalis* [*sic*]) ; 1852, p. 228 ; 1854, p. 1097.
1852 *Semiescharipora interrupta* d'Orbigny, pl. 719, figs. 5–8 ; 1853, p. 487 ; 1854, p. 1098.
1860 *Escharipora chrysalis* d'Orbigny : Coquand, p. 121.
1860 *Semiescharipora interrupta* d'Orbigny : Coquand, p. 150.
1900*a* *Cribrilina interrupta* (d'Orbigny) : Canu, p. 409.
1900*b* *Cribrilina interrupta* (d'Orbigny) : Canu, p. 449.
1900*b* *Escharipora chrysalis* d'Orbigny : Canu, p. 449.
1916*a* *non Pelmatopora interrupta* (d'Orbigny) : Lang, p. 102.
1916*a* *Pelmatopora chrysalis* (d'Orbigny) Lang, p. 102.
1917 *Semiescharipora interrupta* d'Orbigny : Brydone, p. 495.
1919*d* *non Pelmatopora interrupta* (d'Orbigny) : Lang, pp. 211, 223, text-fig. 42.
1919*d* *Pelmatopora chrysalis* (d'Orbigny) : Lang, pp. 212, 223.
1921 *Pelmatopora chrysalis* (d'Orbigny) : Lang, p. xciii.
1921 *Pelmatopora interrupta* (d'Orbigny) : Lang, p. xciii.
1922 *Pelmatopora chrysalis* (d'Orbigny) : Lang, p. 263 [*partim*—D.28438 and D.28439 *excl.*].
1922 *Pelmatopora interrupta* (d'Orbigny) : Lang, p. 281, text-fig. 85.
?1942 *Pelmatopora chrysalis* (d'Orbigny) : Gillard, p. 90.

Emended diagnosis. *Pelmatopora* with unmodified oral spine-bases ; median area of fusion narrow ; pelmatidia apparently absent ; frontal shield flat ; interzooecial secondary tissue abundant, with marked lacunae ; avicularia small, rounded, sporadic, unpaired.

Description. *Zoarium* uni- or bilaminar, now unattached. *Zooecia* elongate, elliptical. *Orifice* higher than wide, evenly rounded distally with straight sides and a straight proximal margin ; slight proximal-lateral constrictions may occur. The outline of the margin of the orifice is apparently somewhat obscured by the accretion of secondary calcareous tissue. Number of *oral spine-bases* indeterminate, probably 4, but obscured by secondary calcareous tissue. *Frontal shield* flat. *Costae* 19–22, closely spaced. No *lateral costal fusions*. Each costa bears a prominent *pelma* near its inner end : these pelmata tend to form a slight " ridge " on either side of the narrow, lens-shaped *median area of fusion*. No *pelmatidia* visible. *Apertural bar* wide, apparently straight and thickened, with a slight median furrow, and probably carrying two large pelmata near the mid-line ; no *median process* present. *Gymnocyst* apparently obscured by plentiful *interzooecial secondary tissue* which fills the interzooecial valleys and contains rather regular, elongate, narrow *lacunae* which are wider at their rounded proximal ends.

Avicularia not very frequent, unpaired, sporadic, small, rounded to slightly elongate. *Ovicells* not seen.

MEASUREMENTS. [Based on Canu's measurements for "*Cribrilina interrupta* (d'Orbigny)", (Canu, 1900*b* : 449).]

Zooecia Lz = 0·92 to 1·00 mm.
lz = 0·42 to 0·50 mm.
hr = 0·24 to 0·26 mm.
lr = 0·17 to 0·21 mm.

REMARKS. Only a photograph (according to Lang, 1922 : 264, the middle specimen of three on a slide labelled "*Escharipora striata* d'Orbigny, Coniacian, Villedieu" in the Canu Collection) is available. The diagnosis and description are based on this photograph (Pl. 9, fig. 7). This specimen compares closely with d'Orbigny's figure of *Escharipora chrysalis* except for the very regular pairing of the avicularia on each zooecium in d'Orbigny's figure.

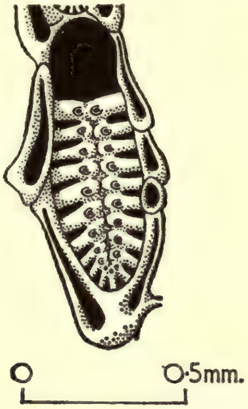


FIG. 58. *Pelmatopora chrysalis* (d'Orbigny). Drawn from a photograph, in the British Museum (Natural History), of the middle specimen of three on a slide labelled "*Escharipora striata* d'Orbigny, Coniacian, Villedieu." F. Canu Collection, Paris.
An adult zooecium and one worn avicularium surrounded by interzooecial secondary tissue with characteristically elongate lacunae.

Canu (1900*b* : 449), who regarded *Semiescharipora interrupta* d'Orbigny and *Escharipora chrysalis* d'Orbigny as synonymous, based his opinion on a comparison of d'Orbigny's actual specimens and gave measurements for the material. Unfortunately he retained the name *interrupta* for the species, although *chrysalis* has priority by one year.

d'Orbigny's figures of both species are highly stylized, but Lang (1922) rigidly interpreted them and disagreed with Canu's conclusions, keeping the two species separate. Lang did not choose a lectotype for *Escharipora chrysalis*, but did so for *Semiescharipora interrupta*. Such rigid interpretation of stylized figures is not desirable, nor is it advisable to choose a lectotype from them in the absence of actual specimens. Canu's conclusions (1900*b*) based on an examination of d'Orbigny's specimens, are therefore accepted in preference to those founded on such questionable interpretations.

D.28438 and D.28439 were labelled by Lang " *Pelmatopora chrysalis* (d'Orbigny) ", but the former has prominently paired, distally pointed and directed avicularia and is here assigned to *P. larva* Lang : the latter has very numerous narrow costae and has been assigned also, with a query, to *P. larva* Lang.

STRATIGRAPHICAL DISTRIBUTION. Senonian, Coniacian of France.

SPECIMENS. None in the collections.

Photograph—the middle specimen of three on a slide labelled " *Escharipora striata* d'Orbigny, Coniacian, Villedieu ". F. Canu Collection.

6. *Pelmatopora larva* Lang

(Pl. 9, fig. 9 ; Text-figs. 59, 60)

1852	*non Semiescharipora interrupta* d'Orbigny, pl. 719, figs. 5–8 ; 1853, p. 487 ; 1854, p. 1098.
?1916*a*	*Pelmatopora interrupta* (d'Orbigny) : Lang, p. 102.
?1919*d*	*Pelmatopora interrupta* (d'Orbigny) : Lang, pp. 211, 223, text-fig. 42.
1921	*Pelmatopora larva* Lang, p. xcv [*nom nud.*].
1922	*Pelmatopora larva* Lang, p. 260, pl. 5, fig. 9 ; text-fig. 77.
1922	*Pelmatopora chrysalis* (d'Orbigny) : Lang, p. 263 [*partim*—D.28438–39 only].

HOLOTYPE. D.28440. Small fragment of unilaminar zoarium, now unattached. Senonian, Coniacian. La Ribochère, Loir et Cher, east of La Chartres-sur-le-Loir, Sarthe, France. F. Canu Collection.

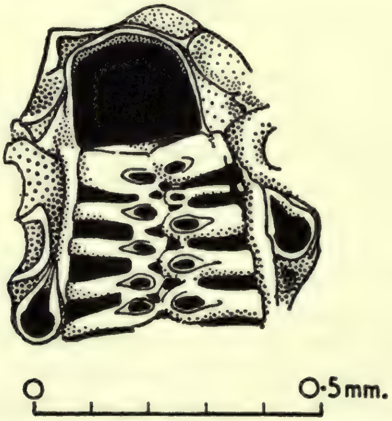


FIG. 59. *Pelmatopora larva* Lang, D. 28438. Distal end of adult zooecium with two distally pointed avicularia, showing their paired occurrence proximal to the orifice.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; median area of fusion narrow ; no pelmatidia ; frontal shield flat ; interzooecial secondary tissue abundant ; avicularia elongate, distally pointed and directed, tending to be paired, one near each proximal-lateral corner of the orifice.

DESCRIPTION. *Zoarium* uni- or bilaminar, now unattached. *Zooecia* elliptical, long and narrow. *Orifice* wider than high, rounded distally with a straight proximal margin, the sides straight or converging slightly proximally. The outline of the margin of the orifice may be slightly obscured by accretion of secondary calcareous tissue. *Oral spine-bases* apparently 4, unmodified, often obscured by secondary calcareous tissue, and not indenting the outline of the orifice. *Frontal shield* flat, of variable length. *Costae* about 17, fairly closely spaced. No *lateral costal fusions.* Each costa bears a large *pelma* near its inner end close to the narrow *median area of fusion.* No *pelmatidia. Apertural bar* wide, but not very thick, bearing two large pelmata very close to the mid-line; there is no *median process. Gymnocyst* almost entirely obscured by plentiful *interzooecial secondary tissue* which fills the intezooecial valleys to a level generally equal to, or a little above, that of the flat frontal shields. Irregular, elongate, shallow *lacunae* occur frequently in the interzooecial tissue, occasionally descending deeply to expose the gymnocyst.

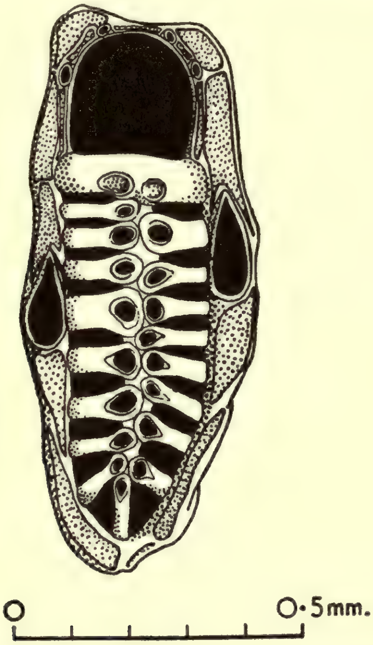


FIG. 60. *Pelmatopora larva* Lang, D. 28440. Holotype. Adult zooecium and two distally pointed and directed avicularia.

Avicularia relatively large, prominent, elongate, distally pointed and directed; generally paired, one near each proximal-lateral corner of the orifice or a little proximal to this position. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·87 to 1·00 mm.
lz = 0·33 to 0·36 mm.
hr = 0·18 mm.
lr = 0·18 to 0·21 mm.
Avicularia Lz = 0·12 to 0·15 mm.
lz = 0·06 to 0·09 mm.

REMARKS. *P. larva* Lang, *P. interrupta* (d'Orbigny) and *P. chrysalis* (d'Orbigny), as interpreted by Lang (1922), have been reconsidered. *P. interrupta* and *P. chrysalis* are synonymous, and *P. larva* is distinguished from them mainly by the type and position of the avicularia. In the holotype of *P. larva*, D.28440, the avicularia always lie proximally to the apertural bar at or near the proximal-lateral corners of the orifice. Nowhere do they occur on the lateral margins of the orifice as in *P. d'orbignyi* Lang, nor are they of the smaller, rounded, sporadic type which are seen in photographs of a specimen here assigned to *P. chrysalis* (d'Orbigny).

D.28438, labelled by Lang " *P. chrysalis* (d'Orbigny) ", also belongs to *P. larva*, for it possesses paired, distally pointed and directed avicularia which lie proximally to the proximal-lateral corners of the orifice. D.28439, similarly labelled by Lang, is also probably better assigned to *P. larva*. Although its costae are constant in number at 21, the dimensions of the zooecia, the well-developed, distally pointed and directed, paired avicularia (one proximal to each proximal-lateral corner of the orifice), and the abundant interzooecial secondary tissue with shallow, elongate lacunae are all features which are more characteristic of *P. larva* than of *P. chrysalis*. The measurements of the specimen are as follows :

Zooecia Lz = 0·87 mm.
lz = 0·36 mm.
hr = 0·15 to 0·18 mm.
lr = 0·18 to 0·21 mm.
Avicularia Lz = 0·15 mm.
lz = 0·09 mm.

STRATIGRAPHICAL DISTRIBUTION. Senonian, Coniacian of France.

SPECIMENS. D.28440. Holotype—see above.

D.28438. Small unattached fragment of bilaminar zoarium, labelled by Lang " *P. chrysalis* (d'Orbigny) ". Horizon, locality and collection as for the holotype.

?D.28439. Small zoarial fragment, now unattached, labelled by Lang " *P. chrysalis* (d'Orbigny) ". Horizon, locality and collection as for the holotype.

7. ***Pelmatopora striata*** (d'Orbigny)

(Pl. 9, fig. 10)

1851	*Escharipora striata* d'Orbigny, pl. 686, figs. 9–12 ; 1852, p. 229 ; 1854, p. 1097.
1851	*Escharipora mumia* d'Orbigny, pl. 687, figs. 4–6 ; 1852, p. 233 ; 1854, p. 1097.
1851	*non Escharipora elegans* d'Orbingy, pl. 684, figs. 13–15 ; 1852, p. 222 ; 1854, p. 1097.
1900*b*	*Cribrilina (Decurtaria) striata* (d'Orbigny) Canu, p. 450.
1900*b*	*non Escharipora elegans* (d'Orbigny) : Canu, p. 457.
1916*a*	*Pelmatopora striata* (d'Orbigny) Lang, pp. 102, 104.
1919*d*	*Pelmatopora striata* (d'Orbigny) : Lang, pp. 212, 222.
1921	*Pelmatopora striata* (d'Orbigny) : Lang, p. xciii.
1922	*Pelmatopora striata* (d'Orbigny) : Lang, p. 264.
?1942	*Pelmatopora striata* (d'Orbigny) : Gillard, p. 90.

LECTOTYPE. (Chosen by Lang, 1922 : 265.) The specimen figured by d'Orbigny, 1851, pl. 686, fig. 10. Néhou, south of Valoignes, east of Ste. Colombe, Manche, France. Senonian.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; apparently no pelmatidia ; frontal shield flat ; about 25 costae.

DESCRIPTION. *Zoarium* uni- or bilaminar, now unattached. *Zooecia* large, elliptical. *Orifice* rounded distally and laterally, with a straight proximal margin, apparently higher than wide. Number and form of *oral spine-bases* not determinable, but definitely not enlarged, probably obscured by the accretion of secondary calcareous tissue. *Frontal shield* apparently flat. *Costae* about 25 or 26, narrow, closely spaced, each with a large *pelma* near its inner end close to the *median area of fusion*. This is somewhat wider than in *P. chrysalis* (d'Orbigny). The outlines of the inner ends of individual costae may be traced into the narrow median area of fusion. No *pelmatidia* and no *lateral costal fusions* visible. *Apertural bar* prominent, rather wide, with a slight median furrow, and with two large pelmata, one on either side of the mid-line. *Gymnocyst* apparently entirely concealed by the very abundant *interzooecial secondary tissue* which completely fills the interzooecial valleys and stands up as ridges between the zooecia. Irregular elongate *lacunae* occur in the secondary tissue.

Avicularia are possibly present but the photograph on which the present diagnosis and description are based is not clear enough to show them with certainty. *Ovicells* not seen.

MEASUREMENTS. [From Canu (1900*b* : 450).]
Zooecia Lz = 1·14 to 1·35 mm.
lz = 0·50 to 0·64 mm.
hr = 0·20 to 0·30 mm.
lr = 0·21 to 0·25 mm.

REMARKS. The diagnosis and description for *P. striata* (d'Orbigny) are only tentative. Canu (1900*b* : 450) based his conclusions on an examination of d'Orbigny's actual specimens and regarded *Escharipora striata* and *E. mumia* as synonymous. This interpretation is followed here, since d'Orbigny's stylized figures have little systematic value.

As Lang has remarked (1922 : 265), there are no indications of pelmata in either of d'Orbigny's figures of the two species which Canu regarded as synonymous, and therefore the placing of *E. striata* in the genus *Pelmatopora* can only be tentative. However, the slide in the Canu Collection, labelled " *Escharipora striata* d'Orbigny ", holds three specimens : the outermost specimens compare closely with the d'Orbigny figures and are definitely *Pelmatopora*. A photograph of one of these outer specimens is in the collections of the British Museum (Natural History). The middle specimen on the slide has been assigned to *P. chrysalis* (d'Orbigny).

STRATIGRAPHICAL DISTRIBUTION. Senonian, Coniacian of France.

SPECIMENS. A photograph only—one of the outer specimens of three on a slide labelled " *Escharipora striata* d'Orbigny, Coniacian, Villedieu ". F. Canu Collection.

8. *Pelmatopora fragilis* (d'Orbigny)

(Pl. 10, figs. 1, 2 ; Text-fig. 61)

1851	*Semiescharipora fragilis* d'Orbigny, pl. 717, figs. 8–11 ; 1853, p. 480 ; 1854, p. 1097.
1885	*Semiescharipora fragilis* d'Orbigny : Vine, pp. 116, 156.
1893	*Cribrilina fragilis* (d'Orbigny) Pergens, pp. 202, 216.
1893	*Cribrilina fragilis* (d'Orbigny) : Vine, pp. 316, 323, 336.
1900*b*	*Cribrilina fragilis* (d'Orbigny) : Canu, pp. 448, 458.
1904	*Cribrilina fragilis* (d'Orbigny) : Jukes-Browne, p. 490.
1916*a*	*Pelmatopora fragilis* (d'Orbigny) Lang, pp. 102, 104.
1916*a*	*Pelmatopora pauciclavia* Lang, pp. 102, 104.
1919*d*	*Pelmatopora fragilis* (d'Orbigny) : Lang, pp. 212, 222.
1919*d*	*Pelmatopora pauciclavia* Lang : Lang, p. 211, text-fig. 41.
1921	*Pelmatopora pauciclavia* Lang : Lang, p. xciv.
1921	*Pelmatopora fragilis* (d'Orbigny) : Lang, p. xcv.
1922	*Pelmatopora pauciclavia* Lang : Lang, p. 267, pl. 5, fig. 11 ; text-fig. 80.
1922	*Pelmatopora fragilis* (d'Orbigny) : Lang, p. 269.
1942	*Pelmatopora fragilis* (d'Orbigny) : Gillard, p. 90.

LECTOTYPE. (Chosen by Lang, 1922 : 269.) The specimen figured by d'Orbigny, 1851, pl. 717, fig. 9. Senonian, Coniacian. Fécamp, Seine Inférieure, France.

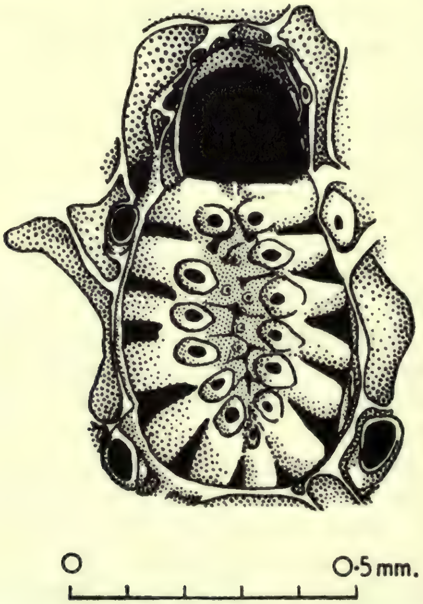


FIG. 61. *Pelmatopora fragilis* (d'Orbigny), D. 28273. Holotype of *P. pauciclavia* Lang. Adult zooecium and paired avicularia. The avicularia at the proximal end belong to adjacent zooecia.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; median area of fusion narrow ; pelmatidia often present ; frontal shield high, flat on top ; costae 9–15 ; orifice relatively large ; avicularia often paired.

Description. *Zoarium* unilaminar, encrusting or now unattached. *Zooecia* broadly oval or with somewhat parallel sides, of variable length. *Orifice* relatively large, usually higher than wide, rounded distally with straight sides and a straight proximal margin. Occasionally the orifice may narrow slightly at the proximal end; there are no proximal-lateral constrictions. *Oral spine-bases* 4, widely spaced, unmodified, possibly very slightly enlarged, but not indenting the outline of the margin of the orifice. *Frontal shield* high, flat on top. *Costae* wide, 9–15 (often 10–11), each with a prominent, raised *pelma* near the inner end at the edge of the median area of fusion: an inner *pelmatidium* is often also present on each costa. *Lateral costal fusions* occur at the level of the pelmata. The area within the pelmata is flat; outside it the costae slope down fairly steeply. *Median area of fusion* narrow. *Apertural bar* thick, prominent, with two large pelmata, one immediately on either side of the mid-line which is marked by a slight median ridge. *Gymnocyst* largely concealed by fairly abundant *interzooecial secondary tissue* which contains irregularly elongate, well-defined *lacunae.*

Avicularia interzooecial, tubular, prominent, often paired one on either side of each zooecium and placed just proximally to the apertural bar, or well proximal to this position. Apparently the avicularian apertures are small, rounded to oval, and, in less worn examples, may be slightly pointed distally. *Ovicells* not seen.

Measurements. [Based partly on Canu's measurements for " *Cribrilina fragilis* (d'Orbigny) ", 1900*b* : 448.]

Zooecia Lz = 0·71 to 0·81 mm.
lz = 0·39 to 0·50 mm.
hr = 0·14 to 0·18 mm.
lr = 0·11 to 0·18 mm.

Remarks. *P. fragilis* was poorly figured by d'Orbigny. Lang (1922 : 269) interpreted the species from a photograph provided by Canu of a specimen in the d'Orbigny Collection. That specimen was one of three on a slide: one of the other two specimens is specifically distinct and was made the type of *P. filliozati* Lang.

Although it is difficult to interpret the photograph of *P. fragilis* it is apparent that the frontal shields are not flat, as suggested by Lang in his diagnosis of the species, but are high and sloping outwards, and that the avicularia tend to occur one on either side of each frontal wall near the apertural bar.

The measurements of the holotype of *P. pauciclavia* Lang, D.28273, are as follows:

Zooecia Lz = 0·78 to 0·81 mm.
lz = 0·39 to 0·47 mm.
hr = 0·18 mm.
lr = 0·15 to 0·18 mm.

The range in number of costae in the specimen is 9–12. Comparing this with the measurements given by Canu (1900*b* : 448) for " *Cribrilina fragilis* (d'Orbigny) ", it is apparent that the dimensions of the two are closely similar. Canu recorded the dimensions of the latter species as Lz = 0·71 to 0·78 mm., lz = 0·42 to 0·50 mm., hr = 0·14 mm. and lr = 0·11 mm. The range in number of costae discernible in the photograph of *Pelmatopora fragilis* is 13–15, and the amount of interzooecial secondary tissue present also compares closely with that in D.28273. D.28452, labelled by Lang " *Pelmatopora ?fragilis* (d'Orbigny) ", is rather badly worn but is tentatively retained in the species. D.28441–42, included in *P. fragilis* by Lang, are, however, here excluded from the species. The former has a flat frontal shield with at least 16 narrow costae, and an amount of interzooecial secondary tissue different from that in *P. fragilis*. Other details are destroyed in this badly damaged specimen and, like D.28442, it is indeterminate.

STRATIGRAPHICAL DISTRIBUTION. Senonian, Coniacian in France, zone of *M. cor-anguinum* in England.

SPECIMENS. D.28452. Worn zoarial fragment encrusting a piece of molluscan shell. Senonian, Coniacian. St. Avertin, south-east of Tours, Indre-et-Loire, France. F. Canu Collection.

D.28273. Holotype of *P. pauciclavia* Lang. Very well preserved zoarial fragment. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed (about 20 ft. above base of zone). East side of Cuckmere Haven, cliffs, Sussex.

Photograph—one of three specimens on a slide labelled " *Cribrilina* [*Semiescharipora*] *fragilis* d'O.". Senonian, Emscherian. Fécamp, Seine Inférieure, France. F. Canu Collection.

Excluded from the species—indeterminate—D.28441, D.28442.

9. *Pelmatopora d'orbignyi* Lang

(Pl. 10, fig. 3 ; Text-figs. 62, 63)

1916*a* *Pelmatopora d'orbignyi* Lang, pp. 102, 104.
1919*d* *Pelmatopora d'orbignyi* Lang : Lang, pp. 211, 222, 225, text-fig. 48.
1921 *Pelmatopora d'orbignyi* Lang : Lang, p. xcv.
1922 *Pelmatopora larva* Lang, p. 260 [*partim*—paratype D.28443 only].
1922 *Pelmatopora d'orbignyi* Lang : Lang, p. 266, pl. 5, fig. 10 ; text-fig. 79.

HOLOTYPE. D.28453. Small fragment of erect, bilaminar zoarium. Senonian, Coniacian. St. Avertin, south-east of Tours, Indre-et-Loire, France. F. Canu Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; pelmatidia occasionally present ; frontal shield flat ; interzooecial secondary tissue abundant ; avicularia prominent, large, distally pointed and directed, paired at the proximal-lateral corners of the orifice.

DESCRIPTION. *Zoarium* unilaminar and probably encrusting, or bilaminar and erect. *Zooecia* long, elliptical, somewhat pointed proximally. *Orifice* higher than wide, evenly rounded distally and laterally with a straight proximal margin, proximal-lateral constrictions variably developed. The outline of the margin of the orifice is somewhat obscured by secondary tissue and is indented laterally by a pair of large avicularia. *Oral spine-bases* probably 4, the distal pair are often visible though somewhat immersed in secondary tissue : the lateral pair, if present, are concealed by the large, lateral, oral avicularia or by secondary tissue. *Frontal shield* apparently flat, the outer ends of the costae descend sharply, but are largely obliterated by the abundant interzooecial secondary tissue. *Costae* 14–20, each with a large *pelma* near the inner end. Some costae may also possess a *pelmatidium* nearer to the mid-line of the zooecium. *Lateral costal fusions* are often present at the level of the pelmata, producing an irregularly developed row of *intercostal spaces* very close to the mid-line and a series of outer intercostal spaces which are slot-like. *Median area of fusion* very narrow and irregular. *Apertural bar* somewhat triangular, wide, but not very thick, with two prominent pelmata one on each side of and close to the mid-line ; a slight median ridge is present, but there is no *median process*. *Gymnocyst* almost entirely concealed by plentiful *interzooecial secondary tissue* which contains irregular but sharply defined elongate *lacunae* through which the smooth gymnocyst may be locally exposed.

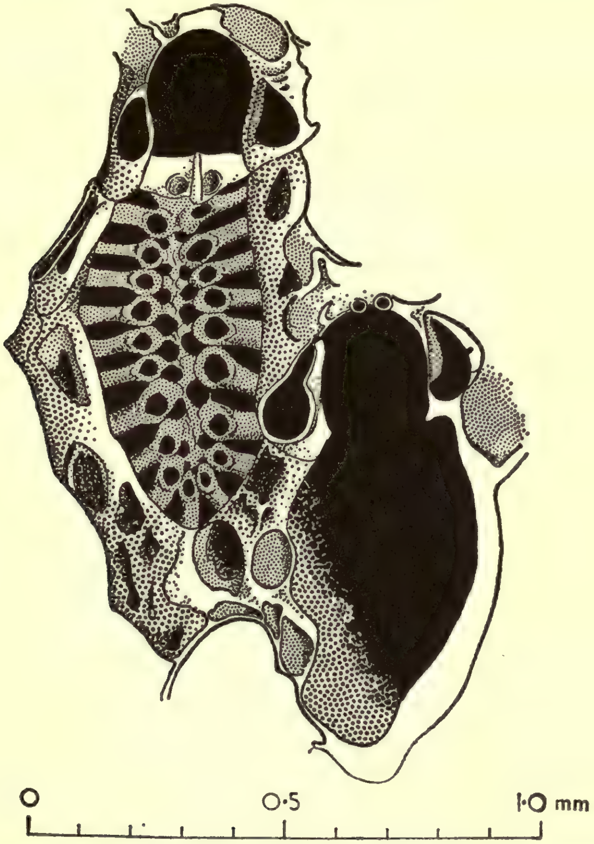


Fig. 62. *Pelmatopora d'orbignyi* Lang, D.28443. Paratype of *P. larva* Lang. Adult zooecium with two worn lateral oral avicularia and adjacent broken zooecium with two well-preserved lateral oral avicularia.

Avicularia prominent, large, paired at the proximal-lateral corners of the orifice, almost as long as the orifice, raised, elongate, pointed, directed distally and obliquely inwards, divided by a *transverse bar* into a larger, rounded, proximal portion and a small, triangular *rostrum*. They are not deeply immersed in the interzooecial secondary tissue. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·94 to 1·15 mm.
lz = 0·46 to 0·50 mm.
hr = 0·21 to 0·24 mm.
lr = 0·15 to 0·18 mm.
Avicularia Lz = 0·15 to 0·24 mm.
lz = 0·12 mm.

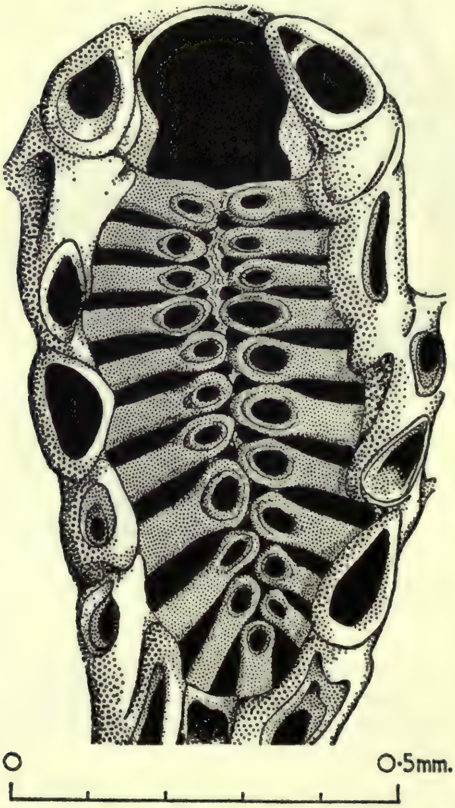


FIG. 63. *Pelmatopora d'orbignyi* Lang, D.28453. Holotype. Adult zooecium and three avicularia surrounded by very abundant interzooecial secondary tissue.

REMARKS. The holotype (D.28453) has been re-examined. D.28443, a paratype of *P. larva* Lang, has been assigned to *P. d'orbignyi* also. Occasional pelmatidia are present on the costae in the median area of the frontal shield in D.28443, and its dimensions and range in number of costae are similar to those of the holotype of *P. d'orbignyi*. D.28443 also has two particularly well-preserved lateral oral avicularia which are large, raised, and distally pointed and directed. Lang described the specimen as " much worn " ; however, it is not as worn as the holotype of *P. d'orbignyi*, in which the avicularia are considerably abraded but regularly paired close to the proximal-lateral corners of the orifice. The position of these avicularia was regarded by Lang as diagnostic for the species, and D.28443 accordingly may be placed in *P. d'orbignyi* Lang.

The holotype has a bilaminar zoarium, but the two laminae of zooecia are not aligned, as is usually the case with normally bilaminar forms, but cross obliquely.

STRATIGRAPHICAL DISTRIBUTION. Senonian, Coniacian of France.

SPECIMENS. D.28453. Holotype—see above.

D.28443. Paratype of *P. larva* Lang. Small fragment of unilaminar zoarium. Coniacian. La Ribochère, Loir-et-Cher, east of La Chartre-sur-le-Loir, Sarthe, France. F. Canu Collection.

10. ***Pelmatopora quadrata*** Lang

(Pl. 10, figs. 4, 5 ; Text-fig. 64)

1916*a* *Pelmatopora quadrata* Lang, pp. 102, 104.
1916*a* *Pelmatopora filliozati* Lang, pp. 102, 105.
1919*d* *Pelmatopora quadrata* Lang : Lang, pp. 197, 211, 222, text-fig. 40.
1919*d* *Pelmatopora filliozati* Lang : Lang, pp. 197, 212, 222.
1921 *Pelmatopora quadrata* Lang : Lang, p. xciv.
1921 *Pelmatopora filliozati* Lang : Lang, p. xciv.
1922 *Pelmatopora quadrata* Lang : Lang, p. 270, text-fig. 81*a*, *b*.
1922 *Pelmatopora filliozati* Lang : Lang, p. 272, text-fig. 81*c*.

HOLOTYPE. D.28271. Well-preserved zoarial fragment with numerous ovicells. The fragment is now unattached. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed (about 20 ft. above base of zone). Cliffs, east side of Cuckmere Haven, Sussex.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; pelmatidia present ; costae 15–20 ; frontal shield well arched ; avicularia elongate, distally pointed and directed, tending to be paired.

DESCRIPTION. *Zoarium* unilaminar, now unattached. *Zooecia* broadly oval, of variable length. *Orifice* wider than high, evenly rounded distally and laterally, with a straight proximal margin ; there are no proximal-lateral constrictions. Where an ovicell is present the orifice is transversely rectangular in outline. *Oral spine-bases* 4, often obscured by the accretion of secondary tissue near the orifice or by the development of ovicells. The oral spines do not indent the outline of the margin of the orifice. *Frontal shield* well arched, but slightly flattened on top in the median area. *Costae* 13–20 (often 15 or 20), each with a prominent *pelma* near the inner end at the edge of the median area of fusion and a *pelmatidium* almost at the extreme inner end. *Lateral costal fusions* occur at the level of the pelmata. *Median area of fusion* of variable width. *Apertural bar* not very wide, relatively flat, with a marked median furrow and carrying a pair of prominent pelmata, one on either side of the mid-line. *Gymnocyst* almost completely concealed by abundant *interzooecial secondary tissue* which lacks well-formed lacunae.

Avicularia not very large, but prominent, distally pointed and directed; a *transverse bar* divides a small, semicircular proximal portion from a long, narrow *rostrum*. There is a strong tendency for the avicularia to be paired, one near each proximal-lateral corner of the orifice; occasional sporadic avicularia also occur.

Ovicells apparently endozooecial, well immersed. Where ovicells are developed a distal oral shield is formed by the infilling of the space between the distal oral spines by a transverse shelf of calcareous tissue. This transverse shelf reduces the size of the orifice which becomes transversely oblong. The lateral pair of oral spines may be displaced proximally, appearing at the distal-lateral corners of the ovicelled orifice and not, as is sometimes the case, obscured by the calcareous tissue.

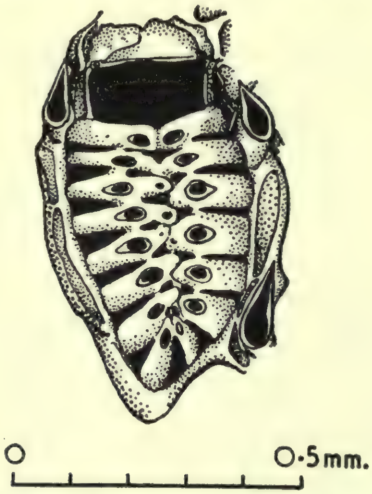


FIG. 64. *Pelmatopora quadrata* Lang, D.28271. Holotype. Ovicelled adult zooecium with paired avicularia. The avicularium at the proximal end belongs to an adjacent zooecium.

MEASUREMENTS. *Zooecia* Lz = 0·81 to 0·85 mm.
lz = 0·39 to 0·43 mm.
hr = 0·12 mm.
lr = 0·15 mm.
Avicularia Lz = 0·15 mm.
lz = 0·09 mm.

REMARKS. The holotype of *P. filliozati* Lang is the specimen nearest to the label on a slide with three specimens from the F. Canu Collection labelled "*Cribrilina* [*Semiescharipora*] *fragilis* d'O." (see Lang, 1922 : 273). A photograph of this specimen is in the collections of the British Museum (Natural History). Careful comparison of this photograph with the holotype of *P. quadrata* Lang shows that the two species are synonymous; in the photograph most zooecia possess 18–20 costae, and in the holotype of *P. quadrata* the range is apparently 13–16, most zooecia having 15 costae. This is the principal difference between the two. Ovicells are developed in the Canu specimen producing the same oblong, modified orifice. The median area of fusion is similar and the avicularia apparently pointed and tending to be paired. It has not been possible to discover the evidence for the measurements which Lang gave for the Canu specimen. The photograph has no scale.

STRATIGRAPHICAL DISTRIBUTION. Senonian, Emscherian in France; zone of *M. cor-anguinum*, *Trochiliopora* Bed, in England.

SPECIMENS. D.28271. Holotype—see above.

D.28272. Paratype. Fragment of a well-preserved, now unattached, zoarium. Horizon, locality and collection as for the holotype.

Photograph of a specimen in the F. Canu Collection. The specimen is mounted nearest to the label on a slide containing three specimens labelled "*Cribrilina* [*Semieschiaripora*] *fragilis* d'O.". The specimen was chosen by Lang as the holotype of his species *Pelmatopora filliozati*. Senonian, Emscherian. Fécamp, north-east of Le Havre, Seine Inférieure, France.

11. ***Pelmatopora fecampensis*** Lang

(Pl. 10, fig. 6; Text-figs. 65–68)

1916*a*	*Pelmatopora fecampensis* Lang, pp. 102, 105.
1919*d*	*Pelmatopora fecampensis* Lang: Lang, pp. 211, 222, text-fig. 43.
1921	*Pelmatopora fecampensis* Lang: Lang, p. xcv.
1922	*Pelamtopora fecampensis* Lang: Lang, p. 286, pl. 6, fig. 3; text-fig. 88.
1958	*Pelmatopora fecampensis* Lang: Didon, pp. 82, 84, text-fig. 9.

HOLOTYPE. D.28473. Zoarial fragment, now unattached. Senonian, Coniacian. Fécamp, north-east of Le Harvre, Seine Inférieure, France. F. Canu Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases; orifice wider than high, larger than in *P. gasteri*; costae 16–21 (often 18 or 19); pelmatidia present; outermost intercostal spaces long and slit-like; interzooecial secondary tissues abundant, lacking well-marked lacunae; avicularia distally pointed and directed, generally two to each zooecium.

DESCRIPTION. *Zoarium* unilaminar, probably encrusting but now unattached. *Zooecia* elliptical, the frontal shields fairly closely spaced. *Orifice* a little wider than high, of very constant size, lacking proximal-lateral constrictions, rounded distally and laterally with a straight proximal margin, its outline not obscured by secondary calcareous tissue. *Oral spine-bases* 4, small and unmodified. *Frontal shield* flatly arched, the *median area of fusion* depressed and narrow. *Costae* 16–21 (often 18 or 19), each with a prominent *pelma* about half-way along its length, coinciding with the edge of the median area. In addition, each costa usually carries a *pelmatidium* closer to the mid-line of the zooecium. *Lateral costal fusions* are developed at the level of the pelmata. *Outermost intercostal spaces* long and slit-like. *Apertural bar* fairly wide, with two large pelmata near the mid-line which is marked by a slight furrow. *Gymnocyst* concealed by abundant *interzooecial secondary tissue* which fills the interzooecial valleys and partly immerses some avicularia. There are usually no well-defined *lacunae* in the interzooecial tissue.

Avicularia small but prominent, distally pointed and directed, the apertures semicircular proximally, narrowing distally into very elongate triangular *rostra*. *Transverse bars* are apparently absent. Very commonly, two variably placed avicularia are associated with each zooecium; occasionally other sporadic avicularia of the same type occur. *Ovicells* apparently endozooecial, but globular and often prominent, tending to reduce the size of the orifice, either obliterating the oral spines or developing apparently within the orifice without displacing the oral spines (Text-figs. 66–68).

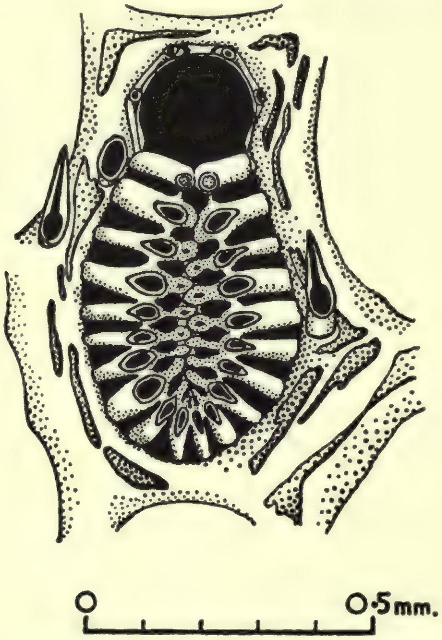


FIG. 65. *Pelmatopora fecampensis* Lang, D. 28473. Holotype.
Adult zooecium and three avicularia.

MEASUREMENTS. *Zooecia* Lz = 0·75 to 0·90 mm.
lz = 0·39 to 0·50 mm.
hr = 0·15 mm.
lr = 0·18 mm.
Avicularia Lz = 0·12 to 0·15 mm.
lz = 0·06 mm.

REMARKS. The holotype and five paratype zoarial fragments of *P. fecampensis* have been re-examined. The avicularia tend to occur regularly, two associated with each zooecium, but they are not constantly developed in the same position. The ovicells, though probably endozooecial, are very prominent and lack the thickened edge characteristic of the endozooecial ovicells of other species, such as *P. somptingensis* Lang and *P. gregoryi* (Brydone).

Paratype D.28472 consists of only four zooecia of normal dimensions one of which is ovicelled. The ovicell is developed apparently within the orifice of the zooecium without displacing the oral spines (Text-fig. 68). Lacunae are quite well developed in the interzooecial secondary tissue of this specimen.

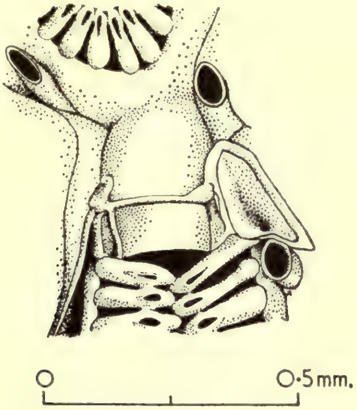


FIG. 66. *Pelmatopora fecampensis* Lang, D. 28475. Paratype. Distal end of ovicelled zooecium, three avicularia, and part of distally adjacent zooecium, the ovicell has a proximally extended calcareous lamina which almost closes the orifice.

Paratypes D.28274 and D.28477 are fragments of zoaria which are now unattached. The former is well preserved with one zoarial lamina encrusting another ; D.28477 is a very small fragment with well-preserved avicularia. D.28476 is another paratype zoarial fragment with only one complete zooecium preserved and no unworn avicularia.

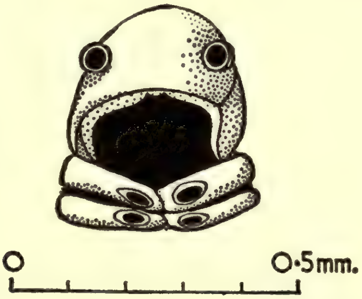


FIG. 67. *Pelmatopora fecampensis* Lang, D.28475. Paratype. Distal end of ovicelled zooecium showing apparent displacement of the lateral oral spines by the ovicell.

Paratype D.28475 is a larger zoarial fragment with prominent oral spine bases and well-preserved avicularia. At least three of its zooecia have ovicells which are apparently endozooecial, but very prominent and globular. In one case the edge of the ovicell is apparently prolonged by a lamina which almost completely closes the orifice, and a thickened, transverse band of tissue runs across the ovicell, possibly marking its normal limit. Several of the zooecia have developed thin calcareous laminae entirely sealing the orifices, and it is possible that the prolongation associated with the ovicell just mentioned is part of such a lamina. In this case the development of the ovicell has obliterated the oral spines, but in an adjacent zooecium two of the oral spines, probably the lateral pair, have been displaced by the development of the ovicell but still remain visible.

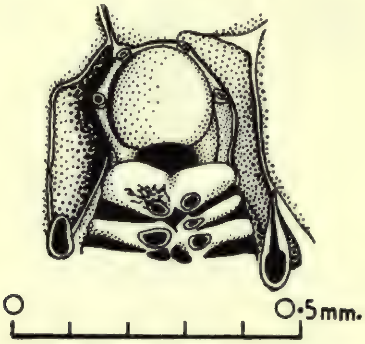


FIG. 68. *Pelmatopora fecampensis* Lang, D.28472. Paratype. Distal end of ovicelled zooecium with two avicularia, showing the apparent development of an ovicell inside the orifice, but not displacing the oral spines.

STRATIGRAPHICAL DISTRIBUTION. Senonian, Coniacian of France.

SPECIMENS. D.28473. Holotype—see above.

D.28472, D.28474–77. Five paratypes. Zoarial fragments now unattached. Horizon, locality and collection as for the holotype.

12. ***Pelmatopora pero*** Lang

(Pl. 10, fig. 7; Text-fig. 69)

1916*a* *Pelmatopora pero* Lang, pp. 102, 105.
1919*c* *Pelmatopora pero* Lang: Lang, p. 107.
1919*d* *Pelmatopora pero* Lang: Lang, pp. 210, 213, 216, 218, 220, 222, text-fig. 52.
1921 *Pelmatopora pero* Lang: Lang, pp. lxiii, xciii.
1922 *Pelmatopora pero* Lang: Lang, p. 290, pl. 6, fig. 5; text-fig. 90 [*partim*—D.29861 *excl.* = *P. brydonei*].
1935 *Pelmatopora pero* Lang: Bassler, p. 165.
1953 *Pelmatopora pero* Lang: Bassler, p. G192, text-fig. 144, 7.

HOLOTYPE. D.23405. Zoarial fragments, now unattached. Senonian, extreme top of zone of *M. cor-anguinum*. Medical College Pit, Epsom, Surrey. F. Möckler Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases; zooecial length about 1·00 mm.; costae 13–20 (often 16–18); two avicularia to each zooecium, usually not symmetrically paired, large, prominent, distally pointed and directed.

DESCRIPTION. *Zoarium* unilaminar, encrusting, but may now be unattached. *Zooecia* elongate, elliptical, tending to be somewhat pointed proximally. *Orifice* wider than high, rounded distally and laterally with a straight proximal margin, of very constant size, without proximal-lateral constrictions. *Oral spine-bases* 4, unmodified, sometimes slightly obscured by secondary tissue. *Frontal shield* flat. *Costae* 13–20 (often 16–18), fairly closely spaced but well defined, each with a prominent *pelma* about half-way along its length and a *pelmatidium* nearer to its inner end. *Lateral costal fusions* are developed at the levels of both the pelmata and pelmatidia, producing a paired row of *intercostal spaces* on either side of the median area. Occasionally a second paired row of irregularly developed intercostal spaces may be present close to the mid-line, when a second series of minute pelmatidia is also developed. The *median area of fusion* is thus of variable width but generally narrow. It is commonly level with, but may occasionally be depressed slightly below, the level of the rest of the frontal shield. *Apertural bar* not very wide, with a very slight median ridge and two indistinct pelmata, one on either side of the mid-line. *Gymnocyst* concealed by plentiful *interzooecial secondary tissue* which almost fills the interzooecial valleys and contains shallow, irregularly elongate depressions.

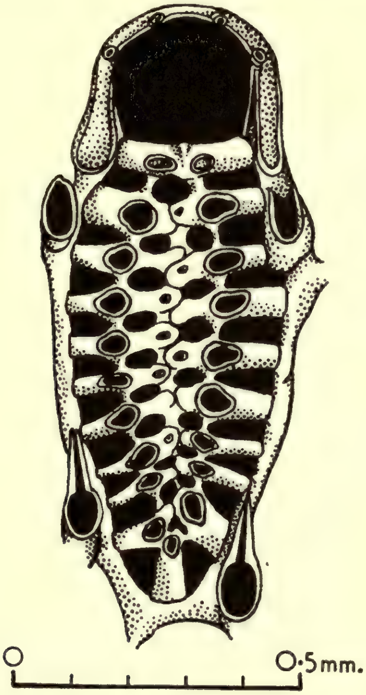


FIG. 69. *Pelmatopora pero* Lang, D. 23411. Paratype. Adult zooecium with paired, damaged avicularia just proximal to the orifice and, at the proximal end, two undamaged avicularia belonging to adjacent zooecia.

Avicularia prominent, large, elongate, distally pointed and directed, rounded proximally with a long, triangular *rostrum*. There are two avicularia to each zooecium, but they are not symmetrically paired. *Ovicells* not seen.

Measurements. *Zooecia* Lz = 0·81 to 1·12 mm.
lz = 0·39 to 0·63 mm.
hr = 0·15 to 0·18 mm.
lr = 0·18 to 0·21 mm.
Avicularia Lz = 0·15 to 0·24 mm.
lz = 0·09 mm.

Remarks. The holotype, fifteen paratypes and two other specimens labelled by Lang *Pelmatopora pero* have been re-examined and retained in this species, but one, D.29861, also labelled as that species, is referred to *P. brydonei* Lang.

Where possible the zooecia of all specimens have been measured. Their dimensions vary considerably, but those of the orifice remain very constant. The avicularia, where unworn, are always elongate and sharply pointed distally. Well-preserved avicularia are present in several specimens, especially in the holotype, and in paratypes D.23404, D.23408–09 and D.23411. Paratype D.23410 possesses lacunae which are more deeply developed than in the other specimens. D.23414 and D.23428 have two definitely paired rows of intercostal spaces in the median area; the inner paired row is imperfectly developed in several zooecia of paratype D.23415. The occurrence of a second paired row of intercostal spaces close to the mid-line is possibly the most variable feature of the species.

All zoarial fragments are now unattached except D.29908 which encrusts a fragment of echinoid test. No young zooecia have been seen.

D.29861 is here assigned to *Pelmatopora brydonei* Lang. It compares closely with the holotype of that species; the distal oral spines of each zooecium are undoubtedly enlarged, the lateral oral spines are visible and unmodified, the length of the zooecia is over 1·00 mm., the paired avicularia are small and oval, and there are 16–20 costae.

Stratigraphical distribution. Senonian, zone of *M. cor-anguinum*.

Specimens. D.23405. Holotype—see above.

D.23402–04, D.23406–16, D 23428. Fifteen paratypes. Zoarial fragments, all now unattached. Horizon, locality and collection as for the holotype.

D.29858. Zoarial fragment, now unattached. Senonian, zone of *M. cor-anguinum*. Pit between Cliff End and Exceat Farm, near Seaford, Sussex.

D.29908. Large fragment of zoarium encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*. Meopham, south of Gravesend, Kent. G. E. Dibley Collection.

D.40744. Zoarial fragment encrusting a piece of echinoid test. Senonian, high in the zone of *M. cor-anguinum*. Pit 264 of Young, Coombs Pit, West Horsley, Surrey.

D.40745–46. Two unattached zoarial fragments. Senonian, zone of *M. cor-anguinum*. Locality and collection as for D.29858.

13. *Pelmatopora suffulta* (Brydone)

(Pl. 10, figs. 8, 9; Pl. 11, fig. 1; Text-figs. 70, 71)

?1911 *Cribrilina insignis* Canu, pp. 252, 280, 282, pl. 6, figs. 7–10.
1913 *Cribrilina suffulta* Brydone, p. 436, pl. 14 [*partim*—fig. 4 only].
?1916*a* *Pelmatopora insignis* (Canu) Lang, pp. 102, 104.
1916*a* *Pelmatopora suffulta* (Brydone) Lang, pp. 102, 104.
1917 *Cribrilina suffulta* Brydone: Brydone, p. 495.
1917 *Cribrilina repleta* Brydone, p. 495 [*partim*—*non* pl. 32, fig. 9].
?1919*d* *Pelmatopora insignis* (Canu): Lang, pp. 211, 218, 222, 224, text-fig. 39.
1919*d* *Pelmatopora suffulta* (Brydone): Lang, pp. 198, 211, 218, 222, 226, text-fig. 45.
1921 *Pelmatopora suffulta* (Brydone): Lang, pp. xciii, xciv.
?1921 *Pelmatopora insignis* (Canu): Lang, p. xciv.
1921 *Pelmatopora repleta* (Brydone) Lang, p. xciv [*nom. nud.*].
1922 *Pelmatopora insignis* (Canu): Lang, p. 273, text-fig. 82.
1922 *Pelmatopora suffulta* (Brydone): Lang, p. 277, text-fig. 83.
1922 *Pelmatopora repleta* (Brydone) Lang, p. 280.
1930 *Pelmatopora repleta* (Brydone): Gaster, table opp. p. 340.

LECTOTYPE. (Chosen by Lang, 1922 : 277.) The specimen figured by Brydone (1913, pl. 14, fig. 4). S.M., B.36262. A large zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*. Gravesend, Kent. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases; costae 14–22; pelmatidia usually present; avicularia small, distally pointed and directed, often paired, one near each proximal-lateral corner of the orifice; interzooecial secondary tissue very variably developed, the gymnocyst may be widely exposed or secondary tissue may almost fill the interzooecial valleys.

DESCRIPTION. *Zoarium* unilaminar, encrusting. *Adult zooecia* usually elongate-oval, some with almost parallel sides; occasionally very wide zooecia occur. *Orifice* rounded distally, often with straight sides, but occasionally somewhat rounded laterally, proximal margin straight, no proximal-lateral constrictions. The outline of the orifice is not obscured either by the oral spines or by secondary calcareous tissue. *Oral spine-bases* 4, possibly very occasionally 5, arranged symmetrically on the distal margin of the orifice. *Frontal shield* variably arched, either low, with a flat, fairly wide, depressed median area, or with fairly steeply sloping costae and a narrower median area; occasionally the whole frontal shield may be flat. *Costae* 14–22, each with a prominent *pelma* about half-way along its length at the edge of the median area, and, nearer the mid-line, a *pelmatidium*. *Lateral costal fusions* always occur at the level of the pelmata producing a paired row of *intercostal spaces*; occasionally, when distinct lateral costal fusions arise also at the level of the pelmatidia, a second row of intercostal spaces may occur in the median area nearer to the mid-line. The *median area of fusion* is narrow and fusiform, or wider with an almost oval outline; it is often depressed below the general surface level of the frontal shield. *Apertural bar* prominent, but not very wide, with two large pelmata, one immediately on either side of the mid-line; there is often a very slight median ridge, but no *median process*. *Gymnocyst* very variably exposed, smooth. *Interzooecial secondary tissue* may be absent in a few cases, but is commonly abundant. Where interzooecial secondary tissue is absent the gymnocyst is widely exposed laterally, and particularly proximally, to the frontal shield. Shallow *lacunae* may be developed in the interzooecial tissue.

Avicularia small, distally pointed and directed, often paired, one near each proximal-lateral corner of the orifice, but sporadic avicularia of the same type also occur frequently. The avicularian aperture is rounded proximally, where it is almost semicircular, and is constricted distally in the triangular *rostrum*. In many specimens the avicularia are worn and apparently oval—it is only when they have not been worn that they retain distally acute rostra.

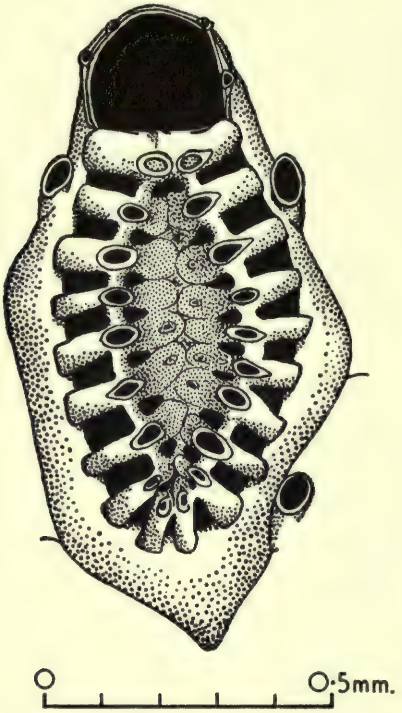


FIG. 70. *Pelmatopora suffulta* (Brydone), 50466 (old collection number). Adult zooecium and three avicularia of specimen labelled by Lang " *P. insignis* (Canu)."

Ovicells apparently endozooecial. When present they are marked by a straight, low distal oral shield which is produced by the infilling with secondary tissue of the space between the distal oral spines. The orifices of ovicelled zooecia thus have an oblong outline.

Young zooecia (of S.M., B.36263) are smaller than the adult zooecia of the same zoarium, but otherwise similar, except that there are fewer costae (10–12), a second series of lateral costal fusions is not present near the mid-line, and the avicularia are not paired.

MEASUREMENTS. *Adult zooecia* Lz = 0·77 to 1·12 mm.
lz = 0·43 to 0·65 mm.
hr = 0·14 to 0·19 mm.
lr = 0·18 to 0·22 mm.

Young zooecia
(measurements based on the young zooecia of S.M., B.36263 only):
Lz = 0·53 to 0·62 mm.
lz = 0·30 to 0·35 mm.
hr = 0·12 to 0·14 mm.
lr = 0·12 to 0·14 mm.

Avicularia
among adult zooecia: Lz = 0·09 to 0·12 mm.
lz = 0·06 mm.

REMARKS. *Pelmatopora suffulta* (Brydone) and *P. repleta* (Brydone) are synonymous. *P. insignis* (Canu) has been doubtfully included in the synonymy and is discussed more fully below.

The specimens, S.M., B.36262–63, which Brydone (1913 : 436, pl. 14, figs. 4, 5) figured as *Cribrilina suffulta*, have been re-examined. The latter specimen, shown in his fig. 5, was later separated by Brydone (1917 : 495) as *Cribrilina repleta*. Lang (1916*a* : 102, 104) placed both specimens in *Pelmatopora suffulta* (Brydone). Subsequently he followed Brydone's separation of the specimens (Lang, 1922 : 280) making S.M., B.36263 the lectotype of *P. repleta* (Brydone). The dimensions and other characters of S.M., B.36262 and S.M., B.36263 are compared below.

	S.M., B.36262 Lectotype of *Pelmatopora suffulta* (Brydone)	S.M., B.36263 Lectotype of *Pelmatopora repleta* (Brydone)
Adult zooecia	Lz = 0·95 to 1·10 mm.	Lz = 0·77 to 0·90 mm.
	lz = 0·43 to 0·65 mm.	lz = 0·43 to 0·53 mm.
	hr = 0·14 to 0·19 mm.	hr = 0·17 to 0·18 mm.
	lr = 0·18 to 0·22 mm.	lr = 0·18 to 0·20 mm.
Avicularia	Lz = Not measurable	Lz = 0·12 mm.
	lz = Not measurable	lz = 0·06 mm.
Number of costae	14–20	14–16.
Oral spine-bases	4	4.
Other characters	Gymnocyst generally widely exposed; interzooecial secondary tissue absent; one (occasionally two) lateral costal fusions on each costa; avicularia usually paired, all worn	Gymnocyst usually concealed; interzooecial secondary tissue plentiful; two (occasionally only one) lateral costal fusions on each costa; avicularia usually paired, distally pointed and directed.

Although the gymnocyst is frequently well exposed in the lectotype of *P. suffulta* there are also numerous zooecia in which it is concealed or only slightly exposed. Conversely, some zooecia in the lectotype of *P. repleta* have exposed gymnocysts. Apart from differences in the amounts of interzooecial secondary tissue which may be developed the two species are clearly similar. Brydone (1917 : 495) said of his species *Cribrilina suffulta* and *C. repleta*, " The relationship between the two is, however, so very close that each is liable to display here and there a considerable measure of the distinguishing character of the other ". This statement is confirmed by an examination of the specimens which Lang assigned to *Pelmatopora suffulta* and to *P. repleta*.

One encrusting zoarial fragment, D.29907, is labelled as an ideotype of *P. suffulta* (Brydone). As in the lectotype, each of its zooecia possesses only four oral spine-bases, not " five in number normally " as suggested by Brydone (1913 : 436). Its avicularia are all worn, but Brydone, basing his opinion on the well-preserved lectotype, rightly stated that the avicularia of *suffulta* correspond " very closely in shape, size and disposition with those of *Cribrilina* [=*Pelmatopora*] *gregoryi*." Some zooecia of D.29907 are ovicelled ; the range in number of costae is 16–18, and the dimensions of the adult zooecia are as follows :

Lz = 0·87 to 0·95 mm.
lz = 0·45 to 0·50 mm.
hr = 0·15 to 0·18 mm.
lr = 0·18 to 0·21 mm.

There are slight amounts of interzooecial secondary tissue.

50466 [Old Collection number], which Lang (1922 : 274) placed in *Pelmatopora insignis* (Canu), is regarded as *P. suffulta* (Brydone), its measurements are :

Lz = 1·00 to 1·12 mm.
lz = 0·45 to 0·59 mm.
hr = 0·15 mm.
lr = 0·18 to 0·21 mm.

The avicularia of 50466 are 0·09 mm. long and 0·06 mm. wide. The main difference from D.29907 is the absence of interzooecial secondary tissue, while the avicularia are more regularly paired. Ovicelled zooecia occur occasionally ; the zoarium is encrusting. The frontal shields of the zooecia are less closely spaced and the gymnocyst generally more widely exposed than in D.29907. Unfortunately the horizon and locality of the specimen are unknown.

D.29857 and D.28275–77, labelled by Lang " *P. repleta* (Brydone) ", are also here referred to *P. suffulta*. The first is a fragmentary encrusting zoarium with a poorly preserved ancestrula and younger zooecia only. Interzooecial secondary tissue is fairly abundant, and each zooecium has about 17 costae and paired avicularia. Describing the avicularia of *P. repleta*, Lang (1922 : 280) referred to them as " sporadically distributed ". They show, however, a strong tendency to be paired, one just proximal to each proximal-lateral corner of the orifice. D.28275–77 are not well preserved, but each zooecium has apparently 16 or 17 costae. Lang (1922 : 281) also recorded as *P. repleta* one other specimen, D.28290, which has 22 costae in some zooecia and a flat frontal shield.

The amount of interzooecial secondary tissue which may be present in a given zoarium is not a useful diagnostic character. The specimens in the British Museum (Natural History), previously recorded by Lang as *P. suffulta* or as *P. repleta*, show particularly the variable amounts of tissue which may occur, both in different parts of the same zoarium and in separate zoaria of otherwise similar specimens. In their development of interzooecial secondary tissue the lectotypes of *P. suffulta* (S.M., B.36262) and *P. repleta* (S.M., B.36263) lie near the extremes of a wide variation which encompasses 50466, D.29907, D.29857, D.28275–77 and D.28290—the other characters of all these specimens being similar, or, as with the range in number of costae which may be present, having a wide variation.

Cribrilina insignis Canu has been doubtfully included in the synonymy of *P. suffulta*, though it is certainly a *Pelmatopora*. The specimen is of Rocanean age, from the type locality of Roca, Argentine. Canu (1911 : 252, pl. 6, figs. 7–10) referred to the zooecia as distinct, separated by deep furrows, large, though the dimensions given are very variable—one of the figured zooecia is 0·50 mm. wide. The range in number of costae is apparently 16–20, and the median area [="plastron" of Canu] is fusiform and " irregularly perforate ". Canu noted, however, that the " perforations " in the median area are aligned with the " prolongation of the intercostal spaces ". There are, in fact, two paired rows of intercostal spaces with others occurring occasionally nearer to the mid-line. It is not possible to discern pelmatidia in Canu's figures—they are certainly present in 50466, which Lang assigned to Canu's species, and which is here referred to *P. suffulta*. The avicularia of *Cribrilina insignis* were described by Canu as oval, not constantly placed, and with small, elliptical somewhat elongate apertures. Although very similar to *P. suffulta*, *P. insignis* (Canu) has narrower zooecia and smaller orifices than those of the former species.

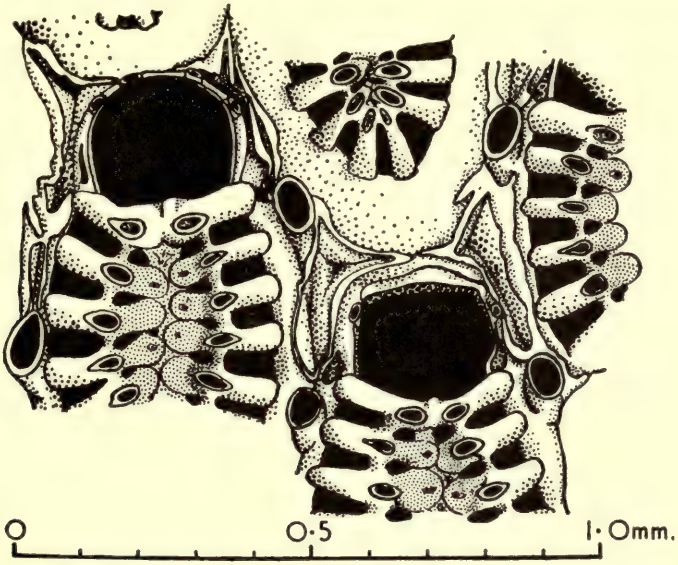


FIG. 71. *Pelmatopora suffulta* (Brydone), D. 29907. Labelled bv Lang " Idiotype ". Parts of five adult zooecia with five worn avicularia : showing the slight amount of interzooecial secondary tissue developed.

It is unfortunate that the horizon of *Cribrilina insignis* Canu is of uncertain age (see p. 19). Feruglio (1949) gave a very full discussion of the conflicting views on the age of the type series of the Rocanean. It has been placed as low as the Cenomanian and as high as the Eocene. The presence of a species of *Pelmatopora*, apparently of the less complex type, possibly suggests a horizon in the Lower Senonian for part, at least, of the type section. However, it is unwise to attempt too firm a comparison of material from such widely separated provinces.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum* in England; Rocanean in Argentina.

SPECIMENS. 50466. Old Collections number. A well-preserved zoarial fragment encrusting a piece of echinoid test. Labelled by Lang "*Pelmatopora insignis* (Canu)". Horizon and locality unknown, possibly Senonian of southern England. Prof. Morris Collection.

D.29907. Zoarial fragment with many broken zooecia encrusting a piece of echinoid test. Labelled by Lang "Ideotype". Senonian, zone of *M. cor-anguinum*. Grays, Essex. G. E. Dibley Collection.

D.29857. Zoarial fragment with poorly preserved ancestrula and young zooecia only, encrusting a shell fragment. Recorded by Lang as *P. repleta* (Brydone). Senonian, zone of *M. cor-anguinum*. Pit in Houndean Bottom, west of Lewes, Sussex.

D.28275–77, D.28290. Four zoarial fragments now unattached. Recorded by Lang as *P. repleta* (Brydone). Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed, about 20 ft. above base of zone. Cliff End, east side of Cuckmere Haven, Sussex.

D.40736. Zoarial fragment encrusting a piece of *Inoceramus* hinge. Senonian, zone of *M. cor-anguinum* (less than 10 ft. below the "strong *cor-anguinum* tabular flint band"). Cliffs, first of Seven Sisters, Cuckmere end, east of Seaford, Sussex.

D.40737–38. Two unattached zoarial fragments. Senonian, zone of *M. cor-anguinum*. Pit between Cliff End and Exceat Farm, east of Seaford, Sussex.

D.40739–41. Three unattached zoarial fragments. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed. Cliffs, Beltout, west of Eastbourne, Sussex.

D.40742. Unattached zoarial fragment. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed. Summit of Downs, Mount Harry, near Lewes, Sussex.

OTHER MATERIAL. S.M., B.36262. Lectotype—see above.

S.M., B.36263. Large, well-preserved zoarial fragment with young and adult zooecia, some with ovicells, encrusting a piece of echinoid test. Figured by Brydone (1913, pl. 14, fig. 5) as *Cribrilina repleta*, chosen by Lang (1922 : 280) as lectotype of *Pelmatopora repleta* (Brydone). Senonian, zone of *M. cor-anguinum*. Gravesend, Kent. R. M. Brydone Collection.

14. ***Pelmatopora simplex*** Lang

(Pl. 11, figs. 2, 3 ; Text-figs. 72, 73)

1916*a*	*Pelmatopora simplex* Lang, pp. 102, 105.	
1919*d*	*Pelmatopora simplex* Lang :	Lang, pp. 210, 218, 221, 224, 226, text-fig. 46.
1921	*Pelmatopora simplex* Lang :	Lang, p. xcii.
1922	*Pelmatopora simplex* Lang :	Lang, p. 282, pl. 6, fig. 1 ; text-fig. 86.
1924	*Pelmatopora simplex* Lang :	Gaster, second of three tables opp. p. 110.
1930	*Pelmatopora simplex* Lang :	Gaster, table opp. p. 340.

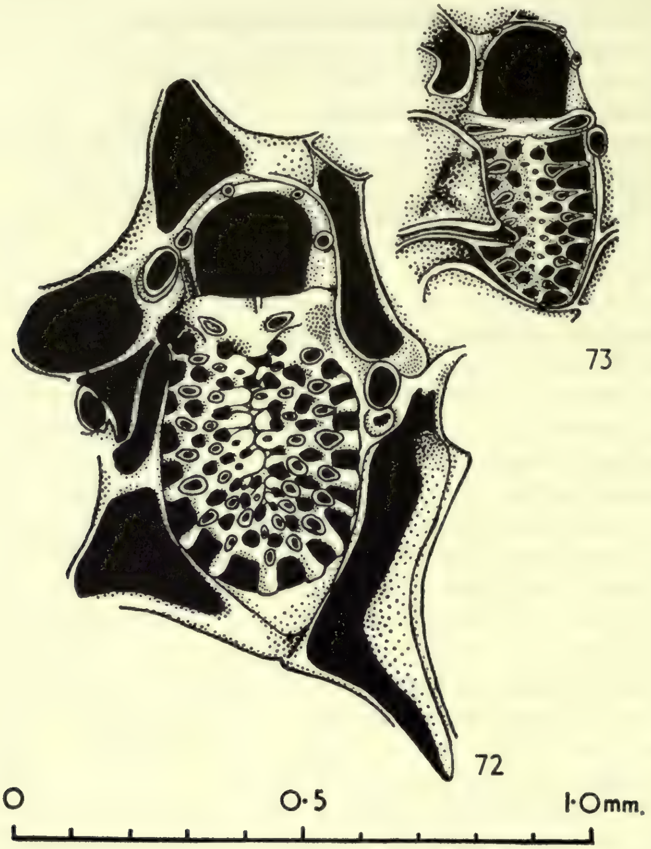
HOLOTYPE. D.28281. Well-preserved zoarium, with ancestrula, encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata.* Cliffs, east side of Old Nore Point, west of Newhaven, Sussex.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases ; Lz less than 1·00 mm. ; costae 16–18 ; a second series of pelmatidia may be developed close to the mid-line ; interzooecial secondary tissue conspicuous, with large, well-defined lacunae ; avicularia paired, one at each proximal-lateral corner of the orifice.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* oval. *Orifice* rounded distally and laterally with a straight proximal margin, without proximal-lateral constrictions ; its outline may be obscured by a high ring of secondary tissue developed particularly on the distal margin. *Oral spine-bases* 4, tending to be obscured by the ring of secondary tissue, the more distal pair slightly enlarged, otherwise unmodified and not completely immersed. *Frontal shield* flat. *Costae* 16–18, well defined, narrow, each with a *pelma* about half-way along its length, and, nearer to the mid-line, at least one, and often two, *pelmatidia. Lateral costal fusions* occur at the levels of the pelmata and pelmatidia, producing two paired rows of *intercostal spaces. Apertural bar* fairly wide, flat, or sloping down towards the proximal edge of the orifice, with two poorly developed pelmata (one near each end), and a very slight median ridge. *Gymnocyst* frequently exposed through the very conspicuous, deep, well-defined, large and irregular *lacunae* in the *interzooecial secondary tissue.* The latter is abundant, and in some cases more than fills the interzooecial valleys, overflowing on to the frontal shields.

Avicularia paired, one near each proximal-lateral corner of the orifice, small, rounded or somewhat elongate, probably distally directed, and usually deeply immersed in the interzooecial secondary tissue. *Ovicells* not seen.

Young zooecia much smaller than the adult zooecia, with smaller, but well-defined, orifices, the margins of which are not obscured by secondary tissue. Oral spine-bases four, small and unmodified. Frontal shield slightly more arched than in the adult zooecia. Costae 11, well defined, narrow, each with a pelma about half-way along its length and a pelmatidium nearer to the mid-line. Lateral costal fusions occur at the level of the pelmata only. Apertural bar very well defined, with a marked pelma near each end. The gymnocyst is exposed through large, irregular lacunae which occur frequently in the plentiful interzooecial secondary tissue. The latter tends to fill the interzooecial valleys and to encroach on to the frontal shields. Avicularia are generally paired, small, round or slightly elongate, and are probably distally directed.



FIGS. 72, 73. *Pelmatopora simplex* Lang, D. 28281. Holotype.

(72) Adult zooecium and three avicularia, showing very deep, large lacunae in the interzooecial secondary tissue.

(73) Young zooecium and avicularium. An expansion of secondary tissue partly obscures the frontal shield.

MEASUREMENTS. *Adult zooecia* Lz = 0·69 to 0·84 mm.
lz = 0·39 to 0·45 mm.
hr = 0·15 to 0·18 mm.
lr = 0·18 mm.
Young zooecia Lz = 0·50 mm.
lz = 0·24 to 0·27 mm.
hr = 0·12 mm.
lr = 0·12 to 0·15 mm.

REMARKS. The holotype and D.29859–60 have been re-examined. The measurements given by Lang (1922 : 282) for adult zooecia of *P. simplex* were slightly overestimated. D.29859 is an encrusting, unilaminar zoarium with a poorly preserved ancestrula. D.29860 is another fragment of a unilaminar encrusting zoarium, probably a young stage. Most zooecia of this specimen are small and have rather more interzooecial secondary tissue than is present in the ancestrular area of the holotype.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *G.* [*A.*] *quadrata* and zone of *O. pilula,* subzone of *E. scutata* var. *depressula* and subzone of *E. scutata* var. *cincta.*

SPECIMENS. D.28281. Holotype—see above.

D.29860. Zoarial fragment with poorly preserved ancestrula, encrusting a piece of echinoid test. Senonian, zone of *O. pilula,* upper part of subzone of *E. scutata* var. *depressula.* Pit 4 of Gaster, west of Boundstone Lane, south of Lancing Ring, north-east of Worthing, Sussex.

D.29859. Zoarial fragment with young zooecia, encrusting a piece of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit on East Hill, Rottingdean, east of Brighton, Sussex.

D.40743. cf. *simplex.* Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit 87 of Gaster, near track to Newlands Barn, north end of East Hill, Rottingdean, east of Brighton, Sussex.

D.40945. Small, well-preserved zoarial fragment with young zooecia, encrusting a piece of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *depressula.* Pit 1 of Gaster, pit near Bridle Road, south of Lancing College and College (or Bunwell's) Farm, west of Pad Farm, Lancing, Sussex.

15. *Pelmatopora plantaris* Lang

(Pl. 11, fig. 4; Text-fig. 74)

1916*a* *Pelmatopora plantaris* Lang, pp. 102, 105.
1919*d* *Pelmatopora plantaris* Lang: Lang, pp. 199, 210, 213, 216, 218, 222, 224, text-figs. 6–8, 51.
1921 *Pelmatopora plantaris* Lang: Lang, p. xciv.
1922 *Pelmatopora plantaris* Lang: Lang, p. 288, pl. 6, fig. 4; text-fig. 89.

HOLOTYPE. D.19620. Zoarial fragment, with young zooecia, encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum.* Wivelrod, west of Alton, Hampshire. H. O. White Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with unmodified oral spine-bases; Lz less than 1·00 mm.; costae 13–16, slightly thicker than in *P. simplex*; a second series of pelmatidia may be developed near the mid-line; interzooecial secondary tissue conspicuous with large well-defined lacunae; two avicularia to each zooecium but not usually symmetrically paired.

DESCRIPTION. *Zoarium* unilaminar, probably encrusting but now unattached. *Adult zooecia* broadly oval. *Orifice* rounded distally and laterally, with a straight proximal margin, without proximal-lateral constrictions; its outline may be obscured by secondary tissue. *Oral spine-bases* 4, unmodified, the distal pair seldom show the slight thickening which is more characteristic of the distal oral spines of *P. simplex. Frontal shield* flat. *Costae* 13–16 (often 14), well-defined, slightly wider than the costae of *P. simplex.* Each costa bears a *pelma* about half-way along its length, and, nearer the inner end, one (occasionally two) *pelmatidia* very close to the mid-line. *Lateral costal fusions* occur at the levels of the pelmata and the outermost pelmatidia producing two paired rows of *intercostal spaces*. *Apertural bar* not quite so wide as in *P. simplex*, with two prominent pelmata and a very slight median furrow. *Gymnocyst* extensively exposed through very conspicuous, deep, large, well-defined, irregular *lacunae* in the abundant *interzooecial secondary tissue*, which occasionally encroaches slightly on to the edges of the frontal shields of some zooecia.

Avicularia, two to each zooecium, but not symmetrically paired as in *P. simplex*, small, rounded (probably by wear), or slightly elongate and probably distally directed; not deeply immersed in the interzooecial secondary tissue. *Ovicells* not seen.

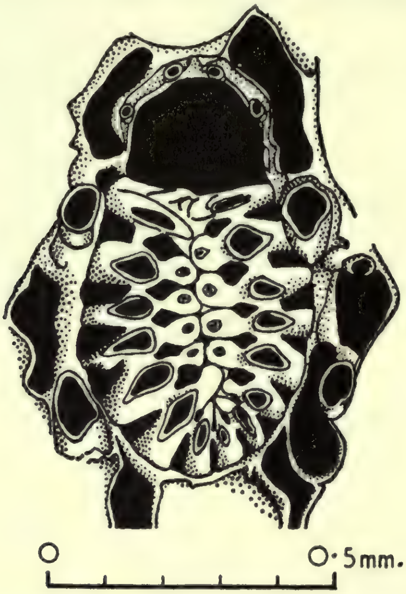


Fig. 74. *Pelmatopora plantaris* Lang, D. 19620. Holotype. Adult zooecium and paired avicularia. The proximal pair belong to adjacent zooecia.

Young zooecia are smaller than the adult zooecia and have more arched frontal shields with fewer (11) costae and less interzooecial secondary tissue; the gymnocyst is more exposed. Avicularia occur singly in the young stages, or there are two associated with each zooecium, although they are not symmetrically paired.

Measurements. *Adult zooecia* Lz = 0·78 to 0·87 mm.
lz = 0·42 to 0·50 mm.
hr = 0·15 mm.
lr = 0·18 mm.
Young zooecia Lz = 0·50 mm.
lz = 0·31 mm.
hr = 0·12 mm.
lr = 0·12 mm.
Avicularia Not measurable.

REMARKS. In the description emphasis has been laid on the differences between *P. simplex* and *P. plantaris*. At most these differences are relatively slight, but there is also a difference in the stratigraphical occurrence of the two species. All the material assigned to *P. simplex* is from the zones of *G.* [*A.*] *quadrata* and *O. pilula*, whereas the material referred to *P. plantaris* is of *M. cor-anguinum* age.

Until more material is available from the intervening horizons it seems advisable to retain the two species as separate, basing the division principally on (i) the lack of symmetrically paired avicularia in *P. plantaris* compared with the common occurrence of evenly placed pairs in *P. simplex*, and (ii) on the smaller number of slightly wider costae in the former compared with the higher number of narrower costae in the latter.

D.28291, an encrusting zoarium, was labelled by Lang " *Pelmatopora ?plantaris* ", but it has 15–17 costae and its avicularia tend to be symmetrically paired.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum.*

SPECIMENS. D.19620. Holotype—see above.

D.28288–89.	Two paratypes, zoarial fragments, now unattached. Senonian, zone of *M. cor-anguinum*, *Trochiliopora* Bed, about 20 ft. above base of zone. Cliffs, east side of Cuckmere Haven, Sussex.
?D.28291.	Zoarial fragment encrusting a piece of echinoid test. Labelled by Lang " *Pelmatopora ?plantaris* ". Senonian, zone of *M. cor-anguinum.* Cliffs, westernmost of Seven Sisters, east of Cuckmere Haven, Sussex.
D.40747.	Incomplete zoarium encrusting a fragment of *Inoceramus* shell. Senonian, zone of *M. cor-anguinum*, 4 ft. below the " strong *cor-anguinum* tabular flint band ". Cliffs, Beltout, west of Eastbourne, Sussex.

16. ***Pelmatopora quadrivolucris*** Lang

(Pl. 11, figs. 5, 6 ; Pl. 12, fig. 1 ; Text-fig. 75)

1913	*Cribrilina gregoryi* Brydone : Brydone, p. 436 [*partim*—pl. 14, fig. 3 only].
1913	*Cribrilina suffulta* Brydone, p. 436 [*partim*—pl. 14, fig. 5 only].
1916*a*	*Pelmatopora quadrivolucris* Lang, pp. 102, 105.
1917	*Cribrilina galanthis* Brydone, p. 495.
1917	*Cribrilina repleta* Brydone : Brydone, p. 495 [*partim*—pl. 32, fig. 9 only].
1919*d*	*Pelmatopora quadrivolucris* Lang : Lang, pp. 200, 213, 216, 222.
1921	*Pelmatopora quadrivolucris* Lang : Lang, p. xciii.
1922	*Pelmatopora quadrivolucris* Lang : Lang, p. 295, text-fig. 92.

HOLOTYPE. D.28907. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum.* Coombs Pit (Pit 264 of Young), West Horsley, north-east of Guildford, Surrey.

EMENDED DIAGNOSIS. *Pelmatopora* with two pairs of exposed enlarged oral spines.

DESCRIPTION. *Zoarium* unilaminar, encrusting, although it may now be unattached. *Zooecia* long, elliptical or almost parallel-sided. *Orifice* rounded distally and laterally with a straight proximal margin ; its outline is often indented by the two pairs of enlarged oral spines, and its size may be reduced by the accumulation of secondary tissue round its margin. *Oral spines* 4, symmetrically arranged in two pairs, all enlarged, and somewhat greater in size than the peg-like distal oral spines of *P. brydonei*. *Frontal shield* flat, of variable length, often just over twice as long as wide. *Costae* 14–19, well defined, each with a *pelma* about half-way along its length and a *pelmatidium* nearer the mid-line; very occasionally a second pelmatidium may occur very close to the mid-line. *Lateral costal fusions* arise at the level of the pelmata, and less frequently at the level of the pelmatidia. *Apertural bar* wide, flat, with two well-defined pelmata. *Gymnocyst* concealed by plentiful *interzooecial secondary tissue* which fills the interzooecial valleys. Slight depressions are present in the surface of the interzooecial tissue.

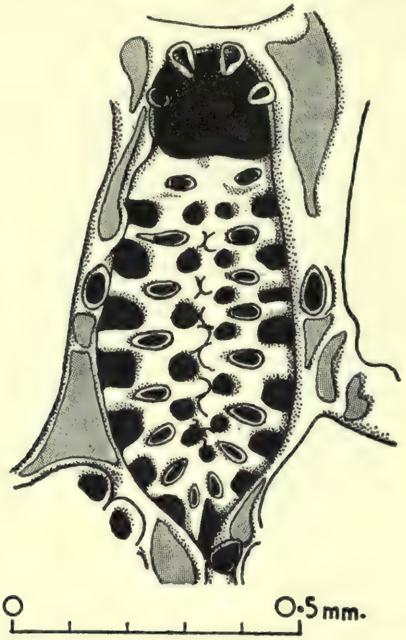


FIG. 75. *Pelmatopora quadrivolucris* Lang, D.28907, Holotype. Adult zooecium with paired, worn avicularia and four enlarged oral spine-bases.

Avicularia distinct, distally pointed and directed, usually paired, one near each proximal-lateral corner of the orifice, occasionally single. The avicularian aperture is constricted distally in the triangular *rostrum* and is wider, almost semicircular, proximally. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 1·00 to 1·25 mm.
lz = 0·35 to 0·60 mm.
hr = 0·15 to 0·21 mm.
lr = 0·21 to 0·27 mm.
Avicularia Lz = 0·12 to 0·15 mm.
lz = 0·07 to 0·09 mm.

REMARKS. D.28907, the holotype, has been re-examined. Five specimens from the R. M. Brydone Collection in the Sedgwick Museum, Cambridge, have also been assigned to the species; these are S.M., B.36261, S.M.,B.36363, S.M., B.71538–39 and S.M., B.75867. The first of these is a well-preserved encrusting zoarium. Part of it was figured by Brydone (1913, pl. 14, fig. 3) originally as *Cribrilina gregoryi*, and later (1917 : 495) distinguished by him as *Cribrilina galanthis*. There is no doubt that it is a specimen of *Pelmatopora quadrivolucris*. Lang (1922 : 293) provisionally included the specimen in his synonymy of *P. brydonei*, presumably basing his opinion on Brydone's figure only. Each zooecium in S.M., B.36261 has four definitely enlarged oral spines, the range in number of costae is 14–16, there is less interzooecial secondary tissue than in the holotype of *P. quadrivolucris*, and the avicularia are more markedly paired, although single avicularia are also frequent. No ovicells or young zooecia are preserved. Part of the zoarial fragment is shown here (Pl. 11, fig. 5).

Brydone (1913 : 436, pl. 14, figs. 4, 5) originally designated *Cribrilina suffulta* [=*Pelmatopora suffulta*] to include his "coarse form" shown in fig. 5. Later (1917 : 495), Brydone separated this coarse form as *Cribrilina repleta* and figured part of another specimen which he also assigned to the latter species. Of this specimen, S.M., B.36363, he stated (1917 : 495, pl. 32, fig. 9) "I have figured an exceptionally well-preserved specimen which shows that the tubercles on the anterior lip [oral spines] are typically four in number, long and tapering, but very brittle". I have re-examined this specimen, each zooecium of which has four enlarged oral spines, and confirm Lang's opinion (1922 : 295 *in synon.*) that it belongs to *Pelmatopora quadrivolucris*. The measurements and other details of the specimen are as follows:

Zooecia Lz = 1·11 to 1·25 mm.
lz = 0·50 to 0·60 mm.
hr = 0·20 to 0·21 mm.
lr = 0·26 to 0·27 mm.
Range in number of costae = 16–19.
Number of lateral costal fusions on each costa = 1 (occasionally 2).
Avicularia Lz = 0·15 to 0·16 mm.
lz = 0·07 to 0·09 mm.

It is noticeable that the dimensions of S.M., B.36363 are generally greater than those of the holotype of *P. quadrivolucris*, suggesting that the latter may be a slightly younger stage of zoarial growth. The avicularia of S.M., B.36363, which are well preserved, are distally pointed and directed, unlike the apparently oval avicularia of the holotype which is somewhat worn. Part of S.M., B.36363 is shown in Pl. 12, fig. 1.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *M. cor-anguinum*.

SPECIMEN. D.28907. Holotype—see above.

OTHER MATERIAL. S.M., B.36261. Holotype (by monotypy) of *Cribrilina galanthis* Brydone. A well-preserved zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *M. cor-anguinum*. Locality 199 of Brydone, siding east of junction, railway cutting, Basingstoke, Hampshire. R. M. Brydone Collection.

S.M., B.36363. Zoarial fragment, now unattached, but partly embedded in a small block of chalk. The specimen figured by Brydone (1917, pl. 32, fig. 9) as *Cribrilina repleta*. Senonian, zone of *M. cor-anguinum*. Locality 559 of Brydone, excavations for tank at fold yard, one quarter mile west of Lower Grenville Copse, Soberton, Hampshire. R. M. Brydone Collection.

S.M., B.71538. Zoarial fragment, now unattached, but partly embedded in a small block of chalk. Senonian, zone of *M. cor-anguinum*. Locality 502 of Brydone, pit in lane one quarter mile south-east of Grasmere Cottage, Easton, Hampshire. R. M. Brydone Collection.

S.M., B.71539. Zoarial fragment, now unattached, but partly embedded in a small block of chalk. Horizon, locality and collection as for S.M., B.36363.

S.M., B.75867. Zoarial fragment encrusting four pieces of echinoid test. Senonian, zone of *M. cor-anguinum*. Locality 328 of Brydone, Hurstbourne Priors (Beehouse Pit), Hampshire. R. M. Brydone Collection.

17. ***Pelmatopora brydonei*** Lang

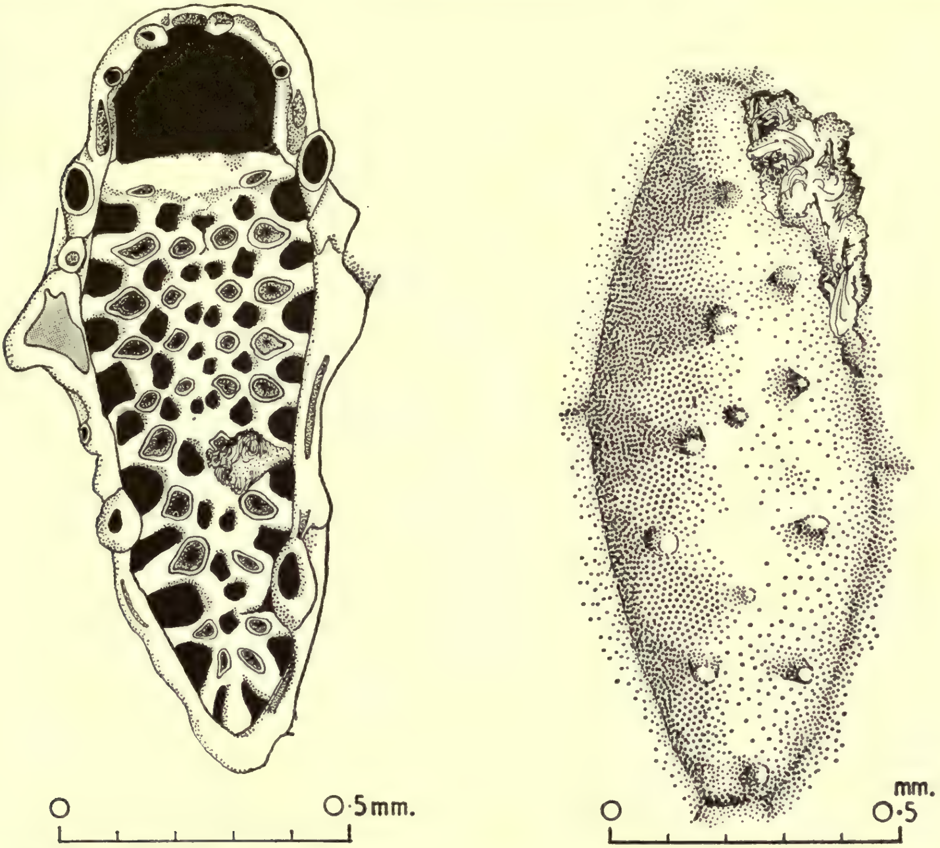
(Pl. 12, fig. 3; Text-figs. 76–78)

1906 *non Cribrilina gregoryi* Brydone, pp. 290, 300, text-fig. 13.
1913 *non Cribrilina gregoryi* Brydone: Brydone, p. 436, pl. 14, figs. 1–3.
1916*a* *Pelmatopora brydonei* Lang, pp. 103, 105.
1917 *non Cribrilina galanthis* Brydone, p. 495.
1919*d* *Pelmatopora brydonei* Lang: Lang, pp. 199, 210, 213, 220, 222, 225, text-figs. 9–11, 53, 54.
1921 *Pelmatopora brydonei* Lang: Lang, p. xciii.
1922 *Pelmatopora brydonei* Lang: Lang, p. 293, text-fig. 91.
1922 *Pelmatopora pero* Lang: Lang, p. 290, pl. 6, fig. 5, text-fig. 90 [*partim*—D.29861 only].
?1958 *Pelmatopora* cf. *brydoneis* [*sic*] Lang: Didon, pp. 83, 85, text-fig. 10.

HOLOTYPE. D.23396. Small zoarial fragment, now unattached. Senonian, top of zone of *M. cor-anguinum*. Epsom, Surrey. F. Möckler Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with a pair of enlarged distal oral spines, the unmodified pair of lateral oral spines not entirely concealed by secondary thickening on the margin of the orifice.

DESCRIPTION. *Zoarium* unilaminar, encrusting, but may now be unattached. *Zooecia* elongate, elliptical, tending to be parallel-sided and somewhat pointed proximally. *Orifice* wider than high, rounded distally and laterally, with a straight proximal margin; the outline of the orifice often indented by the enlarged distal oral spines. Two pairs of *oral spines* visible—the distal pair are enlarged and peg-like and point proximally, the lateral pair are unmodified and almost obscured by the development of secondary tissue. *Frontal shield* variable in length, usually narrow, flat. *Costae* 15–19, well defined, each with a *pelma* about half-way along its length, a *pelmatidium* near its inner end, and, occasionally, a second very small pelmatidium very close to the mid-line. *Lateral costal fusions* occur at the levels of the pelmata and the outermost pelmatidia, producing a paired row of irregular *intercostal spaces* and a variably developed second paired row closer to the mid-line *Median area of fusion* narrow. *Apertural bar* wide and flat, with obscure pelmata.



FIGS. 76, 77. *Pelmatopora brydonei* Lang, D.23396. Holotype.

(76) Very long adult zooecium with normal, enlarged distal oral spines, unmodified lateral oral spine-bases and paired avicularia near the proximal-lateral corners of the orifice. The two more heavily calcified and worn avicularia, near the proximal end of the zooecium, belong to adjacent zooecia.

(77) Dorsal surface of adult zooecium with irregularly spaced solid bosses.

Gymnocyst concealed by plentiful *interzooecial secondary tissue* which fills the interzooecial valleys and which contains slight *lacunae.*

Avicularia distinct, large, distally directed, oval, about two-thirds as wide as long; there is a strong tendency for them to occur near the proximal-lateral corners of the orifice, either singly or paired. Usually two avicularia are associated with each zooecium. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 1·00 to 1·45 mm.
lz = 0·39 to 0·56 mm.
hr = 0·18 mm.
lr = 0·21 mm.
Avicularia Lz = 0·09 mm.
lz = 0·06 mm.

REMARKS. The holotype, eight paratypes, and one other specimen, all labelled by Lang " *P. brydonei* ", have been re-examined.

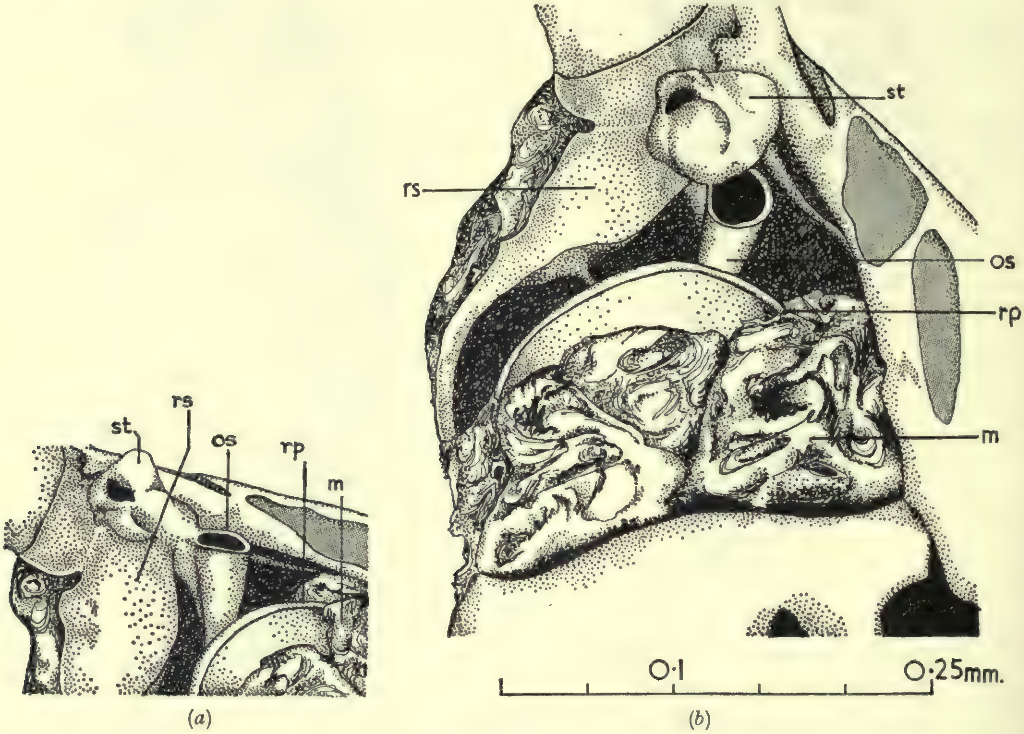


FIG. 78. *Pelmatopora brydonei* Lang, D. 23397. Paratype.
(*a*) Side view of part of a damaged orifice. (*b*) Front view of same orifice. *m*, hard matrix ; *o.s*, apparently unmodified " primary " oral spine ; *r.p*, rim of primary orifice ; *r.s*, rim of secondary orifice ; *s.t*, secondary tissue of enlarged oral spine.

The dorsal surface of the zoarial lamina of the holotype is covered by small, apparently solid, conical bosses which are irregularly distributed and by which the zoarium may have been attached (Text-fig. 77). The form of these dorsal bosses contrasts with the hollow dorsal " spines " developed in *P. gregoryi*, and particularly with those illustrated (Text-figs. 91, 92).

It was stated by Lang (1922 : 294), with reference particularly to D.23397, that " both the right distal apertural [oral] spine and the right secondary aviculoecium are present, the latter lying outside the former. But the primary apertural rim in this specimen is so distinct as to suggest that the whole aperture has been renewed. If this has happened, this specimen cannot be used to demonstrate that the secondary aviculoecium is a new structure, and not a development of the distal apertural spine, as has been assumed hitherto. . . . If the secondary aviculoecia are rightly regarded as developments of no pre-existing structures, the species *P. brydonei* must be considered as arising from a saltation . . . ". Here Lang referred to the nature of the oral spines and orifices of the specimen which is shown here in side and front views respectively (Text-fig. 78*a*, *b*). From a careful examination of the specimen under high-power magnification it is apparent that the rim of the primary orifice is undamaged but partly concealed by hard matrix. Distal to the rim of the primary orifice an apparently unmodified " primary " oral spine is preserved. This structure is, however, intimately fused to a localized accumulation of secondary calcareous tissue on its distal side, here termed " secondary tissue of the enlarged oral spine ". This enlarged oral spine protrudes above the general level of the rim of the secondary orifice which is very much broken, but which normally, in undamaged zooecia, obscures the rim of the primary orifice and the unmodified oral spines. The left-hand distal oral spine has been destroyed.

I regard the smaller " primary " unmodified right-hand distal oral spine and the localized accumulation of secondary tissue on its distal side as parts of the same enlarged distal oral spine which has been broken and worn obliquely along its length. Damage to the distal end of the zooecium has largely removed secondary tissue, exposing the sharply defined distal margin of the primary orifice and the originally small base of the oral spine.

This arrangement does not necessarily indicate renewal of the orifice, but does show that the so-called " secondary aviculoecia " of Lang are, in fact, enlarged oral spines : that is, spines which are developed round the margin of the orifice and which have increased in size during the localized accumulation of secondary tissue.

It is thus incorrect to represent *P. brydonei* (*vide* Lang, 1922 : 295, text-fig. 91) as possessing two pairs of unmodified oral spines in addition to the so-called " secondary aviculoecia ". The species has only one pair of lateral unmodified oral spines and one pair of enlarged distal oral spines. (See also the general remarks on oral spines, p. 35.)

In the adult zooecia of *P. brydonei* the number of costae varies from 15 to 19 and is most often 16. The avicularia, described by Lang as " sporadic ", occur almost invariably two to each zooecium. They are often symmetrically paired, one on either side, near the proximal-lateral corners of the orifice.

D.29861, recorded by Lang (1922 : 292) as *P. pero*, is actually a specimen of *P. brydonei*. The specimen is discussed on p. 150.

STRATIGRAPHICAL DISTRIBUTION. Senonian, upper part of the zone of *M. cor-anguinum*.

SPECIMENS. D.23396. Holotype—see above.

D.23397–401, D.23429–31. Eight paratypes. Zoarial fragments, now unattached. Senonian, extreme top of the zone of *M. cor-anguinum*. Medical College Pit, Epsom, Surrey. F. Möckler Collection.

D.23325. Small zoarial fragment, now unattached. Horizon, locality and collection as for the paratypes.

D.29861. Zoarial fragment encrusting a piece of echinoid test. Recorded by Lang as *P. pero*. Senonian, high in the zone of *M. cor-anguinum*. Coombs Pit (Pit 264 of Young), West Horsley, north-east of Guildford, Surrey.

18. ***Pelmatopora coryli*** (Lang)

(Pl. 12, fig. 4; Text-fig. 79)

1916*a*	*Carydiopora coryli* Lang, p. 94.
1921	*Pelmatopora coryli* (Lang) Lang, pp. xcii, xciii [*nom. nud.*].
1922	*Pelmatopora coryli* (Lang): Lang, p. 285, pl. 6, fig. 2; text-fig. 87.
1923	*Pelmatopora corylii* [*sic*] (Lang): Waters, p. 555.
1924	*Pelmatopora coryli* (Lang): Gaster, second of three tables opp. p. 110.
1930	*Pelmatopora coryli* (Lang): Gaster, table opp. p. 340.

HOLOTYPE. D.28998. Small zoarial fragment of only eight zooecia, encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 2 of Gaster, by reservoir, near Hill Barn, north of North Lancing village, south-east of Lancing Ring, north-east of Worthing, Sussex.

EMENDED DIAGNOSIS. *Pelmatopora* with small zooecia; distal oral spines enlarged, lateral oral spines unmodified and concealed by secondary thickening on the margin of the orifice; costae 11–14; avicularia occasional, sporadic.

DESCRIPTION. *Zoarium* unilaminar, encrusting. *Adult zooecia* small, broadly oval. *Orifice* rounded distally and laterally, with a straight proximal margin, wider than high, not much obscured by secondary tissue. *Oral spines* four, but in the adult zooecia the lateral pair are unmodified and completely covered by secondary tissue. The distal pair of oral spines is enlarged. *Frontal shield* steeply sloping outwards at the margins but flat on top. *Costae* 11–14, each with a *pelma* at the middle and a *pelmatidium* near the inner end. A second pelmatidium may occur occasionally very close to the mid-line. *Lateral costal fusions* are developed at the levels of the pelmata and the outermost pelmatidia, producing two irregularly paired rows of *intercostal spaces*. *Median area of fusion* narrow. The costae are characteristically rounded where they turn down to meet the gymnocyst. *Apertural bar* fairly wide, sloping down to the proximal edge of the orifice, with two very prominent, large pelmata and a very slight median furrow. *Gymnocyst* not exposed. The interzooecial valleys are apparently lined with *secondary tissue*, the edges of this lining tissue standing up as a small but distinct ridge round each frontal shield. The "lacunae" are apparently deep hollows in the interzooecial secondary tissue; they occur only over the deepest parts of the interzooecial valleys.

Avicularia occasional, sporadic, small, rounded, possibly distally directed, frequently much obscured by secondary tissue. *Ovicells* not seen.

Young zooecia smaller than the adult zooecia, with an orifice of the same shape, but with four unmodified oral spines, none of which is obscured by secondary tissue. Frontal shield more often arched, costae 10 or 11, well defined, each with a pelma near the middle and a pelmatidium near the inner end near the mid-line. Only one lateral costal fusion occurs regularly at the level of the pelmata, though lateral fusions may occasionally be developed at the level of the pelmatidia. Apertural bar narrower than in the adult zooecia, with two very large pelmata. The gymnocyst is well exposed proximally to the frontal shield and slightly exposed laterally. Interzooecial secondary tissue, if present, is small in amount and is confined to the region of the orifice. Paired avicularia have been seen associated with only one young zooecium, where they occur one near each proximal-lateral corner of the orifice. Apart from this example, the avicularia occur sporadically in the young zoarial stages.

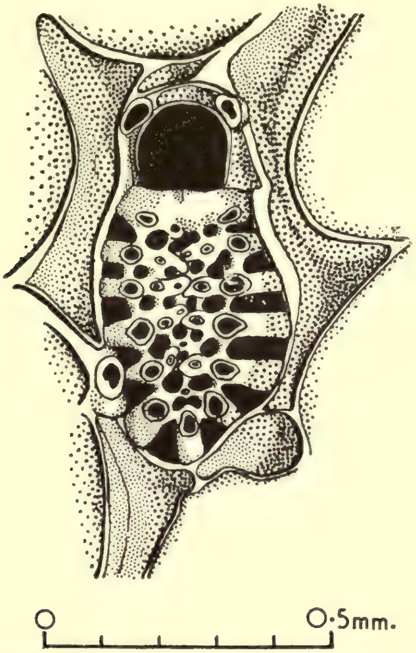


Fig. 79. *Pelmatopora coryli* (Lang), D.28998. Holotype. Adult zooecium with enlarged distal oral spine-bases and single avicularium near the proximal end.

Measurements. *Adult zooecia* Lz = 0·60 to 0·75 mm.
lz = 0·39 to 0·45 mm.
hr = 0·12 to 0·15 mm.
lr = 0·15 to 0·18 mm.
Young zooecia Lz = 0·51 to 0·59 mm.
lz = 0·27 to 0·33 mm.
hr = 0·09 to 0·12 mm.
lr = 0·12 to 0·15 mm.
Avicularia Not measurable.

REMARKS. The holotype and three paratypes, D.28996–97 and D.28999, have been re-examined. In these specimens it is possible to find only one adult zooecium, in the holotype, in which the distal margin of the orifice is complete and unworn. Only three other adult zooecia are present in the holotype—in each case the distal margin is worn but still retains the bases of the enlarged distal oral spines which are well preserved in the unworn adult zooecium. On this evidence the specimen is here grouped with the more complex species of *Pelmatopora* which possess a pair of enlarged distal oral spines. The remaining zooecia of the holotype are smaller, and each has two pairs of unmodified oral spine-bases. It seems probable that Lang based his diagnosis and description on these young zooecia.

In paratype D.28996 only three zooecia retain complete frontal shields and all have worn or damaged distal margins. The zoarium is unilaminar and encrusting. Paired avicularia occur in two of the more complete zooecia, and there are at least two lateral costal fusions arising from each of the 12 or 13 costae which are present. The gymnocyst is variably exposed. The dimensions of this specimen are :

Lz = 0·60 to 0·69 mm.
lz = 0·39 to 0·42 mm.
hr = About 0·12 mm.
lr = 0·15 mm.

Paratype D.28997 is also worn, but there is more abundant interzooecial secondary tissue than in the holotype or in D.28996. The avicularia are generally paired. The adult zooecia are a little larger than in the holotype, with 13 or 14 costae.

D.28999 was labelled by Lang as a paratype of *P. coryli*. It is, however, very badly worn and cannot be placed with certainty in that species. It is the only specimen recorded from the zone of *Marsupites*.

Comparison has also been made between all specimens referred by Lang to *P. coryli* and all species of *Carydiopora* from which it was removed by Lang (1922). None of the remaining species of *Carydiopora* possesses pelmata or distal oral spines typical of *Pelmatopora*.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula* and subzone of *E. scutata* var. *cincta*, and ?zone of *Marsupites* (subzone unspecified).

SPECIMENS. D.28998. Holotype—see above.

D.28996. Paratype. Worn zoarial fragment, encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 4 of Gaster, Western Pit (close to Pit 3 of Gaster), at top of Boundstone Lane, south of Lancing Ring, east of Halewick Lane, Sompting, Sussex.

D.28997. Paratype. Worn zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs, between last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.

?D.28999. Paratype. Very badly worn zoarial fragment. Senonian, zone of *Marsupites* (subzone unspecified). Cliffs, Brighton, Sussex.

19. ***Pelmatopora marsupitorum*** Lang

(Pl. 12, figs. 2, 5 ; Text-figs. 80–83)

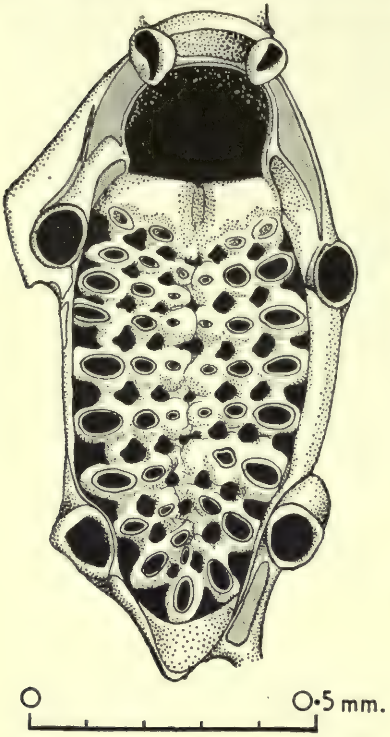
1916*a* *Pelmatopora marsupitorum* Lang, pp. 103, 105.
1916*a* *Pelmatopora roedeanensis* Lang, pp. 103, 105.
1919*d* *Pelmatopora marsupitum* [*sic*] Lang : Lang, pp. 214, 216, 222, text-figs. 55, 56.
1919*d* *Pelmatopora roedeanensis* Lang : Lang, pp. 215, 222.
1921 *Pelmatopora marsupitum* [*sic*] Lang : Lang, pp. xcii, xciii.
1921 *Pelmatopora roedeanensis* Lang : Lang, pp. xcii, xciii.
1922 *Pelmatopora marsupitum* [*sic*] Lang : Lang, p. 297, pl. 6, fig. 6 ; text-figs. 73*b*, 93.
1922 *Pelmatopora roedeanensis* Lang : Lang, p. 299.
1924 *Pelmatopora marsupitum* [*sic*] Lang : Gaster, second of three tables opp. p. 110.
1924 *Pelmatopora roedeanensis* Lang : Gaster, second of three tables opp. p. 110.
1930 *Pelmatopora marsupitum* [*sic*] Lang : Gaster, p. 336, table opp. p. 340.
1930 *Pelmatopora roedeanensis* Lang : Gaster, table opp. p. 340.
?1958 *Pelmatopora* cf. *marsupitum* [*sic*] Lang : Didon, pp. 83, 85, text-fig. 11.

Holotype. D.28867. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites* (subzone unspecified), Brighton, Sussex.

Emended diagnosis. *Pelmatopora* with a pair of relatively short and peg-like enlarged distal oral spines ; the unmodified lateral oral spine-bases always concealed by secondary tissue ; costae 14–20.

Description. *Zoarium* unilaminar, encrusting, but may now be unattached. *Zooecia* elliptical, of variable length. *Orifice* rounded distally and laterally, with a straight proximal margin, its outline often indented by the pair of enlarged distal oral spines. *Oral spines* 4, only the enlarged distal pair visible. Compared with the enlarged distal oral spines of other species these are relatively short and peg-like, occasionally rather broad, and very occasionally tending to widen slightly at their distal ends. The unmodified pair of lateral oral spines is always obscured by secondary tissue accumulated on the margins of the orifice. *Frontal shield* flat, of variable length. *Costae* 14–20 (often 18), well defined, each with a *pelma* near the outer end, a smaller pelma towards the inner end, and often a *pelmatidium* close to the mid-line. *Lateral costal fusions* arise at the levels of the pelmata producing two paired rows of *intercostal spaces*. Occasionally a single line of intercostal spaces may be developed along the mid-line of the frontal shield when opposite intercostal spaces coalesce. Even less frequently, lateral costal fusions may arise at the levels of the pelmatidia giving a third paired row of intercostal spaces. *Median area of fusion* very narrow or absent. *Apertural bar* low and wide, with two well-defined, large pelmata and often with less obvious, smaller pelmata nearer the mid-line. The distal edge of the apertural bar is frequently indented by a minute median furrow. *Gymnocyst* frequently concealed by plentiful *interzooecial secondary tissue* which fills the interzooecial valleys and which contains irregularly elongate *lacunae*.

Avicularia large, prominent, distally pointed and directed, usually paired, one near each proximal-lateral corner of the orifice, but sporadic avicularia of the same type also occur frequently. In unworn avicularia the aperture may be either divided by a straight *transverse bar*, separating a semicircular proximal portion from a triangular *rostrum*, or there may be no transverse bar, the aperture being



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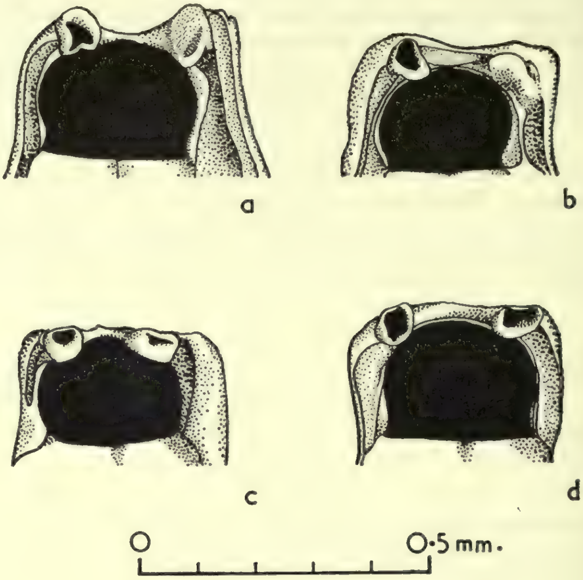

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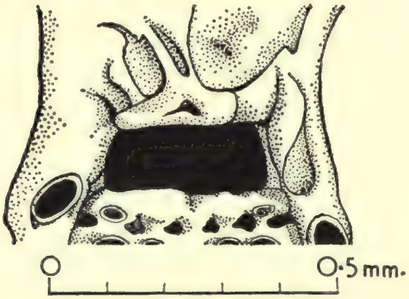

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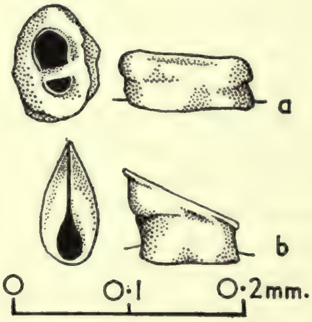


83

FIGS. 80–83. *Pelmatopora marsupitorum* Lang.

(80) D. 39400. Normal adult zooecium with well-preserved enlarged distal oral spines and paired avicularia near the orifice. The two avicularia near the proximal end belong to adjacent zooecia.

(81) Orifices of four adult zooecia showing variation in form of enlarged distal oral spines. The variation is due largely to different degrees of wear: (*a*) D.39400; (*b*) D.39363; (*c*) D.28866, Paratype; (*d*) D.28868, holotype of *P. roedeanensis* Lang.

(82) D. 39363. Orifice with well-buttressed and thickened distal oral shield typical of ovicelled zooecia. Paired, worn, proximal-lateral avicularia are present.

(83) Avicularia. (*a*) D.39369. Somewhat worn, secondarily thickened avicularium with robust transverse bar. (*b*) D. 39400. Well-preserved stalked avicularium.

narrow and slit-like for the distal two-thirds of its length. Unworn avicularia are rare: the commonly worn avicularian aperture has an elongate-oval outline.

Ovicells apparently endozooecial. In ovicelled zooecia the space between the enlarged distal oral spines is infilled with secondary tissue which may project forwards above the distal margin of the orifice forming a prominent distal oral shield. This structure is apparently less pointed than that developed in ovicelled zooecia of *P. somptingensis* and tends to be more solidly buttressed than in that species.

MEASUREMENTS. *Zooecia* Lz = 1·00 to 1·20 mm.
lz = 0·50 to 0·57 mm.
hr = 0·18 mm.
lr = 0·21 mm.
Avicularia Lz = 0·12 mm.
lz = 0·09 mm.

REMARKS. All available specimens recorded by Lang as *P. marsupitorum* or as *P. roedeanensis* have been re-examined. Much additional material, largely from the zone of *G.* [*A.*] *quadrata*, has also been assigned to *P. marsupitorum* as here revised.

Compared with those of *P. brydonei*, the distal oral spines of the holotype of *P. marsupitorum* are more enlarged; they show no tendency to bifurcate as in *P. gregoryi* or in *P. somptingensis*. *P. roedeanensis* is synonymous with *P. marsupitorum*. Lang distinguished the species on possible differences in zoarial growth habit only. The dimensions of the zooecia of *P. roedeanensis* fall within the range of those of *P. marsupitorum* and the two are similar in all other features.

In D.39363 several zooecia possess apparently endozooecial ovicells which are marked by prominent distal oral shields of the type described; the orifices of these ovicelled zooecia are typically oblong.

D.39369 has well worn avicularia of a typically elongate-oval shape. One avicularium is comparatively unworn, with its stout transverse bar preserved and its aperture raised on a robust stalk, the walls of which appear to be thickened by the accretion of secondary tissue. In contrast, the occasionally preserved unworn avicularia of D.39400 apparently lack a transverse bar and their apertures are constricted distally. This form of avicularian aperture seems to be more generally typical of *P. marsupitorum*. Unworn enlarged distal oral spines occur only occasionally. They tend to be triangular in shape, the apex of the triangle pointing towards the centre of the orifice. The shape of the enlarged distal oral spines may vary considerably according to the degree of wear.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *Marsupites* to zone of *G.* [*A.*] *quadrata*, but not yet recorded from the subzone of *E. scutata* var. *cincta* in the zone of *O. pilula*.

SPECIMENS. D.28867. Holotype—see above.

D.28866. Paratype. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for the holotype.

D.28868. Holotype of *P. roedeanensis* Lang. Zoarial fragment now unattached. Horizon, locality and collection as for the holotype.

D.28282, D.28287, D.28869–70. Four zoarial fragments. Horizon, locality and collection as for the holotype.

D.29867. Zoarial fragment. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit 1 of Gaster, south of College Farm, North Lancing, Sussex.

D.29866. Zoarial fragment. Horizon and collection as for D.29867. Cliffs between last groyne east of Rottingdean Gap and Saltdean, Sussex.

?D.28283. Very worn zoarial fragment. Horizon, locality and collection as for D.29866.

D.29868–69. Two zoarial fragments labelled by Lang " *P. roedeanensis* ". Horizon and collection as for D.29867. Cliffs east of Chimney Shaft, Roedean, east of Brighton, Sussex.

D.39363, D.39408. Two zoarial fragments, the former with well-preserved ovicells. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 15 of Gaster, large pit about one-third of a mile south-south-east of Salvington Windmill and north of Hill Cottages, Salvington, Sussex.

D.39369, D.39371, D.39373, D.39376, D.39383. Five zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 20 of Gaster, lower pit on Patching Hill, just above the 200 ft. contour, north of St. John's Church, Patching, Sussex.

D.39386–88. Three zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit by track, near 200 ft. contour, south-east of Walderton, west side of Walderton Down, West Sussex.

D.39393, D.39403, D.39433–34. Four zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 26 of Gaster, South Woodleighs Pit, east of gravel pit, north-east of Woodleigh Lodge, about half a mile west of Pit 24 of Gaster, Warningcamp, north-east of Arundel, Sussex.

D.39398–99. Two zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 18 of Gaster, Old Lime Kiln, north-west corner of Munery's Copse, west of Pit 17 of Gaster, east end of Clapham Wood, Sussex.

D.39400. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 19 of Gaster, on western boundary of Church Copse, west of St. Mary's Church, Clapham, Sussex.

D.40707. Very large zoarial fragment encrusting a piece of echinoid test. Senonian, zone and subzone of *Marsupites*. Section 75 of Gaster, cliffs, east of Brighton, Sussex.

D.40708–10. Three zoarial fragments now unattached. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Section 85 of Gaster. Roedean Cliffs, east of Brighton, Sussex.

D.40711–17. Seven zoarial fragments encrusting pieces of echinoid test. Horizon, locality and collection as for D.40707.

D.40973. *Pelmatopora* cf. *marsupitorum*. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Section 113 of Gaster, cliffs, Rottingdean to Lower Bannings, east of Saltdean Cottages, Sussex.

D.41036.	Zoarial fragment encrusting large cyclostomatous polyzoan. Horizon, locality and collection as for D.40973.
D.41037.	Very large zoarial fragment encrusting part of an echinoid test. Horizon, locality and collection as for D.40973.
D.41038–40.	Three zoarial fragments encrusting pieces of echinoid test. Horizon, locality and collection as for D.40973.
D.41042.	Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.40708.
D.41047–49.	Three zoarial fragments encrusting pieces of echinoid test. Horizon, locality and collection as for D.29867.
D.41050–55.	Six zoarial fragments, now unattached. Horizon, locality and collection as for D.29867.
D.41056–57	Two zoarial fragments encrusting pieces of echinoid test Horizon, locality and collection as for D.40973.

20. ***Pelmatopora gregoryi*** (Brydone)

(Pl. 13 ; Pl. 14, figs. 1–4 ; Text-figs. 84–94)

1852	*non Semiescharipora simplex* d'Orbigny, pl. 718, figs. 1–4 ; 1853, p. 481 ; 1854, p. 1097 [*vide* Lang].
?1900	*Cribrilina* sp. : Rowe, p. 341 [*partim*—special undescribed form], [*vide* Lang].
1906	*Cribrilina gregoryi* Brydone, pp. 290, 300, text-fig. 13 [*partim*—specimens from zone of *G.* [*A.*] *quadrata* only, *caet. excl.*].
1910	*Cribrilina gregoryi* Brydone : Brydone, p. 77.
?1910	*Cribrilina* sp. : White, p. 56 [*vide* Lang].
?1910	*Cribrilina simplex* (d'Orbigny) : White, p. 55 [*vide* Lang].
?1911	*Cribrilina gregoryi* Brydone : Griffith & Brydone, p. 4.
?1912	*Cribrilina gregoryi* Brydone : Brydone, pp. 20, 53, 62, 70, 89–95.
?1912	*Cribrilina gregoryi* Brydone : White, pp. 35, 43.
1913	*Cribrilina gregoryi* Brydone : Brydone, p. 436, pl. 14, figs. 1, 2 [*partim*—*non* fig. 3].
?1913	*non Cribrilina gregoryi* Brydone : White, p. 24 [*vide* Lang].
?1913	*Cribrilina gregoryi* Brydone : White, pp. 27, 30, 32, 38 [*partim*—*vide* Lang].
1913	*Cribrilina gregoryi* Brydone : Lang, p. 171 [*partim*—specimens other than D.23963 from zone of *G.* [*A.*] *quadrata* only : *caet. excl.*].
1916*a*	*Pelmatopora gregoryi* (Brydone) Lang, pp. 103, 106.
1916*a*	*Pelmatopora bidens* Lang, pp. 103, 106.
1916*a*	*Pelmatopora lancingensis* Lang, pp. 103, 106.
1916*a*	*Pelmatopora promontoriorum* Lang, pp. 103, 106.
1916*a*	*Pelmatopora collium* Lang, pp. 103, 106.
1916*a*	*Pelmatopora saltdeanensis* Lang, pp. 103, 106.
1916*a*	*Pelmatopora ranunculoides* Lang, pp. 103, 106.
1916*a*	*Pelmatopora lacuum* Lang, pp. 103, 106.
1916*a*	*Pelmatopora gyrinoides* Lang, pp. 103, 106.
1917	*Cribrilina gregoryi* Brydone : Brydone, pp. 50, 52, 495 [*partim*].
1919*d*	*Pelmatopora gregoryi* (Brydone) : Lang, pp. 215, 221.
1919*d*	*Pelmatopora bidens* Lang : Lang, pp. 214, 221, text-figs. 61, 62.
1919*d*	*Pelmatopora lancingensis* Lang : Lang, pp. 214, 221, text-figs. 63, 64.
1919*d*	*Pelmatopora promontoriorum* Lang : Lang, pp. 214, 221, text-fig. 67.
1919*d*	*Pelmatopora collium* Lang : Lang, pp. 214, 221, text-fig. 68.
1919*d*	*Pelmatopora saltdeanensis* Lang : Lang, pp. 214, 221, 224, 226, text-figs. 65, 66.

1919*d* *Pelmatopora ranunculoides* Lang : Lang, pp. 214, 221, text-figs. 69, 70.
1919*d* *Pelmatopora lacuum* Lang : Lang, pp. 214, 221, text-fig. 71.
1919*d* *Pelmatopora gyrinoides* Lang : Lang, p. 214, text-fig. 72.
1921 *Pelmatopora gregoryi* (Brydone) : Lang, p. xci.
1921 *Pelmatopora bidens* Lang : Lang, pp. xci, xcii.
1921 *Pelmatopora lancingensis* Lang : Lang, pp. xci, xcii.
1921 *Pelmatopora promontoriorum* Lang : Lang, pp. xci, xcii.
1921 *Pelmatopora collium* Lang : Lang, p. xcii.
1921 *Pelmatopora saltdeanensis* Lang : Lang, p. xcii.
1921 *Pelmatopora ranunculoides* Lang : Lang, pp. xcii, xciii.
1921 *Pelmatopora lacuum* Lang : Lang, p. xcii.
1921 *Pelmatopora gyrinoides* Lang : Lang, p. xcii.
1922 *Pelmatopora gregoryi* (Brydone) : Lang, p. 304 [*partim*—*non* D. 8009, D.28537, D.21169].
1922 *Pelmatopora bidens* Lang : Lang, p. 311, pl. 6, fig. 8, text-figs. 73*f*, 97.
1922 *Pelmatopora lancingensis* Lang : Lang, p. 314, pl. 6, fig. 9 ; text-figs. 73*g*, 98.
1922 *Pelmatopora saltdeanensis* Lang : Lang, p. 316, text-fig. 99.
1922 *Pelmatopora collium* Lang : Lang, p. 319, text-fig. 100.
1922 *Pelmatopora promontoriorum* Lang : Lang, p. 320, pl. 6, fig. 10.
1922 *Pelmatopora ranunculoides* Lang : Lang, p. 321, pl. 6, fig. 11, text-fig. 101.
1922 *Pelmatopora lacuum* Lang : Lang, p. 324.
1922 *Pelmatopora gyrinoides* Lang : Lang, p. 324, pl. 6, fig. 12 ; text-fig. 102.
1924 *Pelmatopora bidens* Lang : Gaster, second of three tables opp. p. 110.
1924 *Pelmatopora lancingensis* Lang : Gaster, second of three tables opp. p. 110.
1924 *Pelmatopora collium* Lang : Gaster, second of three tables opp. p. 110.
1924 *Pelmatopora promontoriorum* Lang : Gaster, second of three tables opp. p. 110.
1924 *Pelmatopora ranunculoides* Lang : Gaster, second of three tables opp. p. 110.
1924 *Pelmatopora lacuum* Lang : Gaster, second of three tables opp. p. 110.
?1924 *Cribrilina gregoryi* Brydone : White, pp. 55, 62.
?1929 *Cribrilina gregoryi* Brydone : Brydone, pp. 9, 12, 13.
1929 *Pelmatopora gregoryi* (Brydone) : Lang, p. 437.
1930 *Pelmatopora gyrinoides* Lang : Gaster, table opp. p. 340.
1930 *Pelmatopora ranunculoides* Lang : Gaster, table opp. p. 340.
1930 *Pelmatopora bidens* Lang : Gaster, table opp. p. 340.
1930 *Pelmatopora lancingensis* Lang : Gaster, table opp. p. 340.
1930 *Pelmatopora saltdeanensis* Lang : Gaster, table opp. p. 340.
1930 *Pelmatopora collium* Lang : Gaster, table opp. p. 340.
1930 *Pelmatopora promontoriorum* Lang : Gaster, table opp. p. 340.

LECTOTYPE. (Chosen by Brydone, 1913 : 436.) S.M., B.36120. The specimen figured by Brydone (1906 : 300, text-fig. 13). Senonian, zone of *G.* [*A.*] *quadrata*. Pit 1092 of Brydone, large pit in Stakes' Lane, Upham, Hampshire. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with a pair of distally elongated, pointed, somewhat slender, enlarged distal oral spines which tend to bifurcate, the " outer horn " of the bifurcation curving away laterally and proximally ; interzooecial secondary tissue abundant, often tending to stand out as a ridge above the flat frontal shield.

DESCRIPTION. *Zoarium* unilaminar, encrusting or may now be unattached, occasionally (in parts at least) erect or cylindrical. *Adult zooecia* oval to elliptical with somewhat parallel sides. *Orifice* wider than high, rounded distally and laterally, with a straight proximal margin, its outline indented by the pair of enlarged distal oral spines. Only the distal pair of 4 *oral spines* are visible in the adult zooecia. The distal oral spines are enlarged, elongated, generally pointed and somewhat slender, lengthened in an outwardly curving fashion, or tending to bifurcate, the " outer horn " of the bifurcation curving towards the lateral or proximal margins of the orifice, and the " inner horn" only slightly developed. Other unmodified oral spines, if present, are always entirely concealed by the accumulation of secondary tissue round the margin of the orifice. *Frontal shield* of variable length, flat. *Costae* 11–20 (often 13–16), well defined, each with two *pelmata* and a *pelmatidium*. *Lateral costal fusions* occur at the levels of the pelmata, producing two paired rows of *intercostal spaces*. The *outermost intercostal spaces* vary in shape from slot-like to oval. *Median area of fusion* very narrow. *Apertural bar* wide and low, often sloping down to the proximal margin of the orifice, with conspicuous pelmata on its proximal edge. *Gymnocyst* concealed by abundant *interzooecial secondary tissue* which fills the interzooecial valleys, often standing up as ridges above the general level of the commonly flat frontal shields. Irregular *lacunae* are variably developed in the interzooecial tissue.

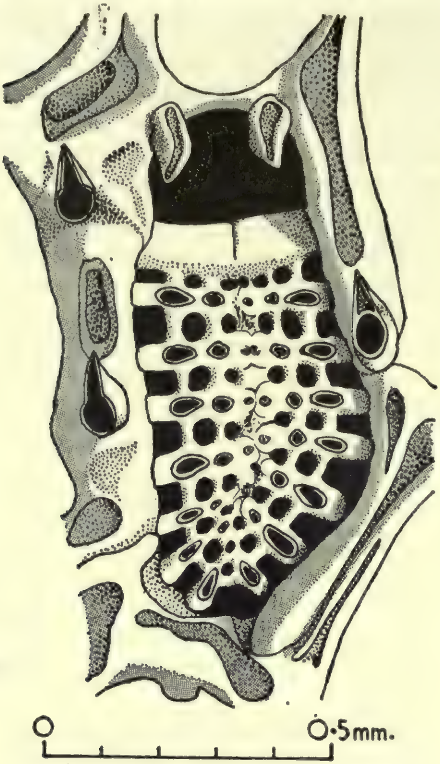
Avicularia prominent, distally pointed and directed, usually regularly paired, one near each proximal-lateral corner of the orifice. The avicularian aperture is almost circular proximally, narrowing distally to a triangular *rostrum*, and usually without a transverse bar ; the aperture is often raised on a stout stalk (Text-fig. 94). Occasionally sporadic avicularia of the same type also occur.

Ovicells endozooecial. In ovicelled zooecia the space between the enlarged distal oral spines is infilled with secondary tissue producing a prominent distal oral shield, which is apparently less pointed than that developed in *P. somptingensis*.

Young zooecia small, but with a relatively large orifice which is wider than high, with two pairs of oral spine-bases which are slightly enlarged but otherwise unmodified. Apertural bar more rounded and narrower than in the adult zooecia, with two very prominent pelmata and with a slight proximal bend in the mid-line. Costae 10–13, each with a pelma and, in some, an inconspicuous pelmatidium nearer to the mid-line. Frontal shield more arched than in the adult zooecia. Small, sporadic avicularia may be present in the circum-ancestrular area in which secondary interzooecial tissue is lacking. Secondary tissue may, however, encroach on to the young zooecia from the adult stages of the same zoarium.

MEASUREMENTS. *Adult zooecia* Lz = 0·75 to 1·20 mm.
lz = 0·40 to 0·50 mm.
hr = 0·15 to 0·18 mm.
lr = 0·21 mm.
Young zooecia Lz = About 0·50 mm.
lz = About 0·33 mm.
hr = 0·12 to 0·15 mm.
lr = 0·13 to 0·15 mm.

[*continued on* p. 180.



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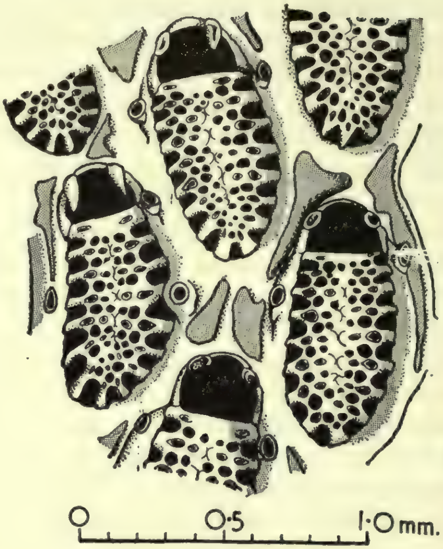

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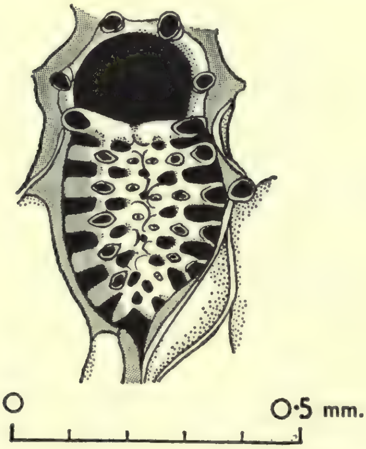

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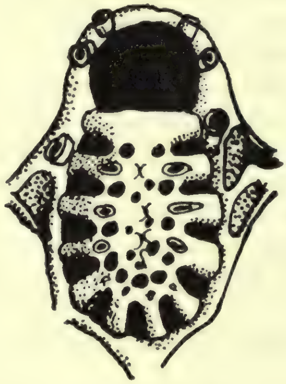

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Scale as for Fig. 84.

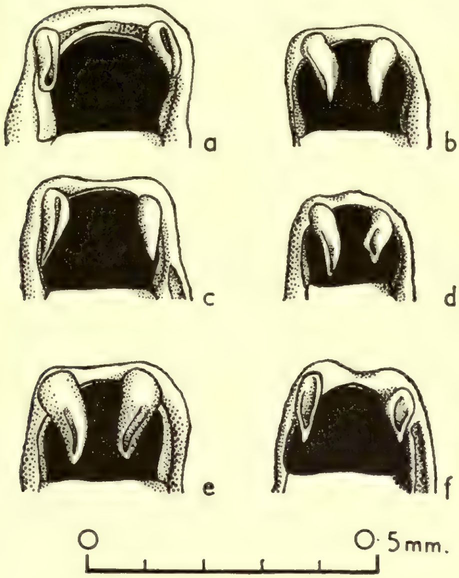
Figs. 84–87. *Pelmatopora gregoryi* (Brydone).

(84) S.M. B.36120. Lectotype. Adult zooecium with lengthened, enlarged distal oral spines and three avicularia surrounded by plentiful interzooecial secondary tissue with lacunae.

(85) S.M. B. 36120. Lectotype. Ancestrula with one small, rounded lateral avicularium.

(86) D.39414. Part of encrusting zoarium with plentiful interzooecial secondary tissue which is smooth with shallow lacunae. The avicularia and most of the enlarged distal oral spines are worn.

(87) D.39414. Young zooecium of the circum-ancestrular area. Two small, worn avicularia are present near the proximal-lateral corners of the orifice.



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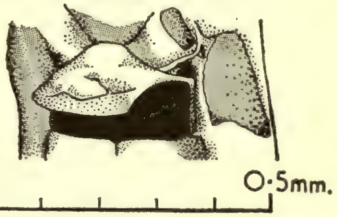

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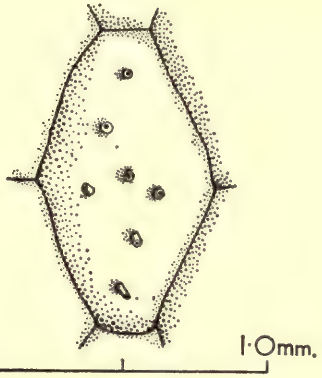

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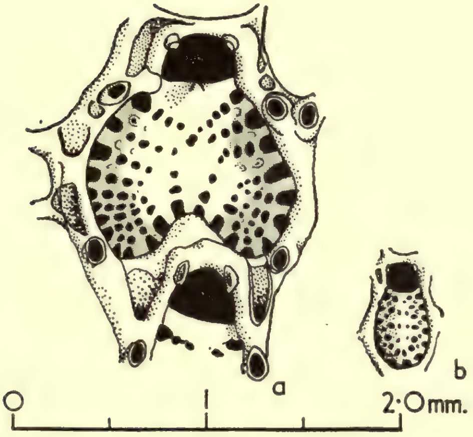

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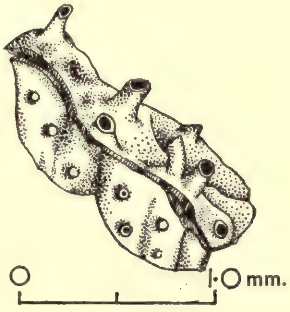

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FIGS. 88–92. *Pelmatopora gregoryi* (Brydone).

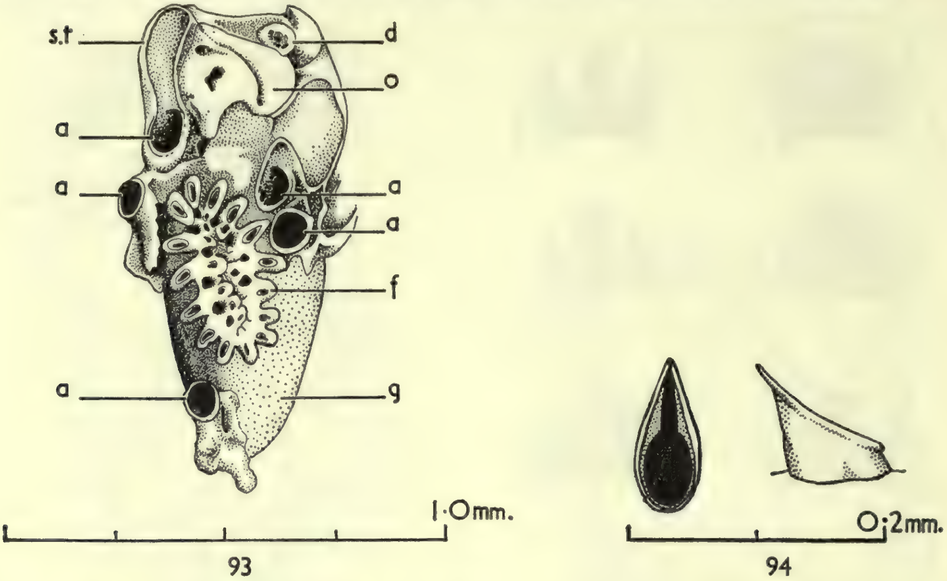
(88) Orifices of six adult zooecia showing variation in form of enlarged distal oral spines. The variation is due largely to different degrees of wear: (*a*) and (*c*) D.28947, holotype of *P. lancingensis* Lang; (*b*), (*d*) and (*e*) D.28820, paratype of *P. promontoriorum* Lang; (*f*) D. 28934, holotype of *P. bidens* Lang.

(89) D. 39046. Orifice of adult ovicelled zooecium with markedly thickened and projecting distal oral shield.

(90) (*a*) D. 39301. Abnormal adult zooecium produced by coalescence of buds of two adjacent rows of zooecia. The orifice of the proximally adjacent zooecium and seven worn avicularia are also shown; (*b*) D.39301. Young zooecium from circum-ancestrular area.

(91) D.39301. Dorsal surface of normal adult zooecium with irregularly spaced small, hollow spines.

(92) D.39301. Enlarged dorsal spines developed along the line of a fracture in the basal zooecial wall.



FIGS. 93–94. *Pelmatopora gregoryi* (Brydone).

(93) D.39382. Aborted adult zooecium. *a*, avicularia; *d*, worn, enlarged distal oral spine; *f*, distorted frontal shield; *g*, very prominent gymnocyst; *o*, heavily calcified infilling of orifice; *s.t*, distal extension of tongue of interzooecial secondary tissue covering distal oral spine.

(94) D.28816. Paratype of *P. lancingensis* Lang. Unworn avicularium.

Ancestrula of lectotype Lz = 0·45 mm.
lz = 0·30 mm.
hr = 0·12 mm.
lr = 0·13 mm.
Avicularia Lz = 0·12 to 0·15 mm.
lz = 0·06 to 0·07 mm.

REMARKS. The lectotype of *Pelmatopora gregoryi* (Brydone), S.M., B.36120, is a very well preserved, unilaminar, encrusting zoarium with young zooecia. The adult zooecia possess enlarged distal oral spines of the type described. The range in number of costae is 12–15, and the outermost intercostal spaces slot-like. The avicularia are prominent, regularly paired, distally pointed and directed; the pointed rostrum may be separated from the proximal part of the aperture by a slight transverse bar which is frequently distally curved—more often there is no bar between the rostrum and the proximal part of the avicularian aperture. A few zooecia are ovicelled; in these the distal oral shield produces a markedly oblong, transversely elongate orifice. The dimensions of the lectotype are:

Adult zooecia Lz = 0·87 to 1·06 mm.
lz = 0·45 to 0·50 mm.
hr = 0·15 to 0·18 mm.
lr = 0·21 mm.

Young zooecia Lz = 0·48 to 0·50 mm.
lz = 0·32 to 0·34 mm.
hr = 0·12 to 0·14 mm.
lr = 0·13 mm.
Avicualaria Lz = 0·13 mm.
lz = 0·06 to 0·07 mm.

Pelmatopora bidens, P. lancingensis, P. promontoriorum, P. collium, P. saltdeanensis, P. ranunculoides, P. lacuum and *P. gyrinoides*, all species established by Lang, are here grouped together as synonymous with *P. gregoryi.*

Lang originally interpreted the lectotype of *P. gregoryi* (Brydone) from Brydone's 1906 and 1913 descriptions and figures. Unfortunately these do not show the form of the enlarged distal oral spines. Examination of the actual specimen shows that they are not, as Lang (1922 : 305) has stated, " very much flattened distally and distinctly bilobed ", but are of the distally elongate curved form described above. This feature, and the range in number of the costae, the form of the avicularia, and the nature and amount of secondary tissue, are all similar to those of *P. bidens* Lang, which is thus synonymous with *P. gregoryi.* In addition the other seven species of *Pelmatopora* mentioned above are all synonymous with *P. bidens* and are thus all junior synonyms of *P. gregoryi.*

P. saltdeanensis Lang is morphologically similar to *P. promontoriorum* Lang and was maintained as separate solely on supposed differences in zoarial growth habit. Similarly, Lang separated *P. lacuum* from *P. ranunculoides.*

P. gyrinoides was established by Lang as a separate encrusting species only on the evidence of a single, somewhat worn zooecium : it might equally well be a young zooecium of *P. ranunculoides.* The latter species is morphologically similar to *P. promontoriorum* : the general range in number of costae is very similar (11–16 for *ranunculoides* and 12–19 for *promontoriorum*), the zooecia of the latter are generally more slender than those of the former species, but this may be a reflection of differences in growth habit (see remarks on the Recent species *Steganoporella buskii* Harmer, p. 22).

In turn, *Pelmatopora promontoriorum* is synonymous with *P. bidens* : they have the same general range in number of costae (11–19 and 12–20 respectively) and are similar in other features.

P. collium was established by Lang on the basis of its apparently more plentiful, ridge-like interzooecial secondary tissue and on its supposedly fewer costae, but both of these features may be very variable even in a single zoarium.

Lang divided the remaining species, *P. lancingensis,* from *P. bidens* primarily on the nature of the enlarged distal oral spines. But he stated that in *P. bidens* these structures vary " much and, apparently, irregularly, in individual development " from small and peg-like to large and more elongate. In his description of *P. lancingensis,* he referred to the enlarged distal oral spines as " varying somewhat and, apparently, irregularly in amount of development, but generally large, elongate . . ". The number of costae in both species is very similar. It was suggested by Lang (1922 : 315) that the avicularia of *P. lancingensis* have " somewhat blunt apertures ", whilst those of *P. bidens* he described (1922 : 312) as having apertures

" divided by a constriction into a proximal more-or-less circular portion and a rostrum, which is more-or-less triangular, sometimes rather blunt, and sometimes rather acutely pointed ". Here Lang was evidently comparing worn and unworn avicularia. The unworn avicularia of both species are distinctly pointed and of very similar form. Apparent variation in the form of the enlarged distal oral spines is due almost entirely to different degrees of wear ; as with the avicularia, the enlarged distal oral spines of both species, when unworn, are very similar in form. The two species are therefore regarded as synonymous.

In these terms, *Pelmatopora gregoryi* is seen to be a species with a relatively wide range of morphological variation which includes the eight species discussed above, many of which have identical horizons and localities.

Many specimens from the C. T. A. Gaster Collection, particularly from the zone of *G.* [*A.*] *quadrata*, have been assigned to *Pelmatopora gregoryi* as revised here. D.39406 possesses some ovicelled zooecia with well-developed distal oral shields (Text-fig. 89). D.39414 and D.39301 are well-preserved encrusting zoarial fragments with young zooecia (Text-figs. 87, 90*b*). An abnormal growth-form of zooecium occurs in D.39301 (Text-fig. 90*a*), it is possibly produced by the coalescence of the buds of two adjacent rows of zooecia. The dorsal surface of each zooecium of D.39301 is covered by a variable number of small, hollow bosses. These may become lengthened into small, hollow spines possibly affording extra means of attachment to damaged parts of the zoarium (Text-figs. 91, 92).

Some very unusual aborted zooecia are present in D.39382 : in the figured example (Text-fig. 93), the avicularia appear to be duplicated, the orifice is almost completely sealed by secondary calcareous tissue, and the frontal shield is much distorted, with the gymnocyst showing very prominently. A worn proximally placed avicularium is also present.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *Marsupites* to *G.* [*A.*] *quadrata*.

SPECIMENS. D.28934, D.28828–35, D.28933. Holotype and nine paratypes of *P. bidens* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit 2 of Gaster, by reservoir, near Hill Barn, North Lancing, north-east of Worthing, Sussex.

D.28987. Paratype of *P. bidens* Lang. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 10 of Gaster, western pit, in lane east of Charman Dean, north of Worthing, Sussex.

D.28796, D.29873–78. Seven paratypes of *P. bidens* Lang. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 9 of Gaster, eastern pit, lane east of Charman Dean, north of Worthing, Sussex. D.28796—T. H. Withers Collection.

D.28968–70. Three paratypes of *P. bidens* Lang. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 7 of Gaster, pit in Upton Lane (Lambleys Lane), Sompting, north-east of Worthing, Sussex.

D.28804–05. Two paratypes of *P. bidens* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit on East Hill, Rottingdean, east of Brighton, Sussex.

D.21168. Paratype of *P. bidens* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit north-west of Chilton Candover, west of Alton, Hampshire. L. Treacher Collection.

D.28953–58. Six paratypes of *P. bidens* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit 4 of Gaster, west of Boundstone Lane, south of Lancing Ring, north-east of Worthing, Sussex.

D.28963–64. Two paratypes of *P. bidens* Lang. Horizon as for D.28953–58. Pit 5 of Gaster, Dankton Lane, north-east of Sompting Church, north-east of Worthing, Sussex.

D.7315. Large zoarial fragment labelled by Lang " *P. bidens* ". Senonian, zone of *G.* [*A.*] *quadrata*. Arreton Down, south of Newport, Isle of Wight. Miss M. Salter Collection.

D.29097. Three fragments of the same zoarium labelled by Lang " *P. bidens* ". Senonian, zone of *G.* [*A.*] *quadrata*. Portsdown, Hampshire. W. Gamble Collection.

D.23992–24001. Ten zoarial fragments labelled by Lang " *P. bidens* ". Senonian, zone of *G.* [*A.*] *quadrata*. Newhaven, Sussex. F. Möckler Collection.

D.29865. Zoarial fragment labelled by Lang " *P. bidens* ". Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Large pit on Warningcamp Hill, north-east of Arundel, Sussex.

D.28947, D.28946, D.28948–50. Holotype and four paratypes of *P. lancingensis* Lang. Senonian, zone of *O. pilula*, upper part of subzone of *E. scutata* var. *depressula*. Pit 3 of Gaster, east of Boundstone Lane, south of Lancing Ring, north-east of Worthing, Sussex.

D.28285–86. Two paratypes of *P. lancingensis* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs, east side of Rottingdean Gap, near and above the last groyne, east of Brighton, Sussex.

D.28962. Paratype of *P. lancingensis* Lang. Horizon, locality and collection as for D.28963–64.

D.28808–19, D.28923–29. Nineteen paratypes of *P. lancingensis* Lang. Horizon, locality and collection as for D.28934.

D.4337. Zoarial fragment labelled by Lang " *P. lancingensis* ". Senonian, zone of *G.* [*A.*] *quadrata*. East Harnham, south of Salisbury, Wiltshire. W. Gamble Collection.

D.29874–75. Two zoarial fragments labelled by Lang " *P. lancingensis* ". Horizon, locality and collection as for D.28953.

D.29055. Zoarial fragment with ovicelled zooecia, labelled by Lang " *P. lancingensis* ". Senonian, zone of *G.* [*A.*] *quadrata*. Locality and collection as for D.28796.

D.29871–73. Three zoarial fragments labelled " *P. lancingensis* ". Horizon, locality and collection as for D.28947.

D.28842, D.28841, D.28843–44. Holotype and three paratypes of *P. saltdeanensis* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs, between last groyne east of Rottingdean Gap and Saltdean, east of Brighton, Sussex.

D.28538. Paratype of *P. saltdeanensis* Lang. Senonian, zone of *G.* [*A.*] *quadrata*. Southern England. F. H. Butler Collection.

D.21171. Zoarial fragment labelled by Lang " *P. saltdeanensis* ". Senonian, zone of *G.* [*A.*] *quadrata*. Compton, south-west of Winchester, Hampshire. L. Treacher Collection.

D.28824, D.28825–27. Holotype and three paratypes of *P. collium* Lang. Horizon, locality and collection as for D.28934.

D.28823. Paratype of *P. collium* Lang. Horizon, locality and collection as for D.28842.

D.28284. Zoarial fragment labelled by Lang " *P. collium* ". Horizon, locality and collection as for D.28842.

D.28930, D.28836–40, D.28849–52, D.28871–73, D.28931–32. Holotype and fourteen paratypes of *P. promontoriorum* Lang. Horizon, locality and collection as for D.28934.

D.28959–61. Three paratypes of *P. promontoriorum* Lang. Horizon, locality and collection as for D.28953.

D.28951–52. Two paratypes of *P. promontoriorum* Lang. Horizon, locality and collection as for D.28947.

D.28806–07, D.28874, D.28877. Four paratypes of *P. promontoriorum* Lang. Horizon, locality and collection as for D.28842.

D.28876. Paratype of *P. promontoriorum* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Cliffs, east side of Telscombe Cliff Staircase, east of Brighton, Sussex.

D.28820–22. Three paratypes of *P. promontoriorum* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Cliffs, east of Old Nore Point, west of Newhaven, Sussex.

D.28967. Paratype of *P. promontoriorum* Lang. Horizon, locality and collection as for D.28968.

D.28972. Paratype of *P. promontoriorum* Lang. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 8 of Gaster, between Upton Lane (Lambleys Lane) and east of Charman Dean, north of Broadwater, Worthing, Sussex.

D.28856, D.28857–59, D.28845–48. Holotype, three paratypes and four zoarial fragments of *P. ranunculoides* Lang. Horizon, locality and collection as for D.28842.

D.28864. Paratype of *P. ranunculoides* Lang. Horizon, locality and collection as for D.28934.

D.28860. Paratype of *P. ranunculoides* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Upper part of pit on East Hill, Rottingdean, east of Brighton, Sussex.

D.28861. Paratype of *P. ranunculoides* Lang. Senonian, zone of *Marsupites* [subzone unspecified]. Brighton, Sussex.

D.28875. Zoarial fragment labelled by Lang " *P. ranunculoides* ". Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Cliffs, west side of Saltdean Bottom, east of Brighton, Sussex.

D.28279. Zoarial fragment labelled by Lang " *P. ranunculoides* ". Senonian, zone of *G.* [*A.*] *quadrata.* Cliffs, between Rottingdean and Saltdean, east of Brighton, Sussex.

D.28280. Zoarial fragment labelled by Lang " *P. ranunculoides* ". Senonian, zone of *G.* [*A.*] *quadrata.* Saltdean, east of Brighton, Sussex.

D.10995. Two fragments of the same zoarium labelled by Lang " *P. ranunculoides* ". Rottingdean, east of Brighton, Sussex. H. D. Schloss Collection.

D.28862, D.28863, D.28938–43, D.28935–37, D.28853–55. Holotype and seven paratypes of *P. lacuum* Lang, and six zoarial fragments labelled by Lang " *P. lacuum* ". Horizon, locality and collection as for D.28934.

D.28270. Holotype of *P. gyrinoides* Lang. Senonian, zone of *G.* [*A.*] *quadrata.* Saltdean, west of Newhaven, Sussex.

D.39340–41, D.39344, D.39348, D.39351–52, D.39357, D.39359–60, D.39366, D.39368, D.40057. Twelve zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 15 of Gaster, large pit about one-third of a mile south-south-east of Salvington Windmill, north of Hill Cottages, Salvington, Sussex.

D.9425. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata.* Locality unknown. Caroline Birley Collection.

D.19564. Zoarial fragment—specimen presented by H. O. White, said to be identical with that described by him as a *Cribrilina,* resembling the sole of a hob-nailed boot (White, 1910 : 56). Senonian, zone of *G.* [*A.*] *quadrata.* Southampton Waterworks Pit, Otterbourne, south of Winchester, Hampshire. H. O. White Collection.

D.39379, D.39382. Two zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 20 of Gaster, lower pit on Patching Hill, north of St. John's Church, just above the 200 ft. contour, Patching, Sussex.

D.39389. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata.* Pit by track, near 200 ft. contour, south-east of Walderton, west side of Walderton Down, West Sussex.

D.39401, D.40058. Two zoarial fragments. Horizon, locality and collection as for D.28796.

D.39405, D.40059–63. Six zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* South Woodleighs Pit, east of gravel pit, north-east of Woodleighs Lodge, about half a mile west of Pit 24 of Gaster, Warningcamp, north-east of Arundel, Sussex.

D.39406. Zoarial fragment, some zooecia ovicelled. Senonian, zone of *G.* [*A.*] *quadrata.* Labelled as " Material from Pits 17, 18, 19, 24 and 32 " of Gaster—all in the zone of *G.* [*A.*] *quadrata.*

D.39412, D.40064. Two zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Labelled as " Material from Pits 8, 11, 15, 16, 17 and 23 " of Gaster—all in the zone of *G.* [*A.*] *quadrata.*

D.39414–15, D.40065–66. Four zoarial fragments. Senonian, ?zone of *G.* [*A.*] *quadrata.* Locality uncertain.

D.39301. Zoarial fragment with some aborted zooecia. Senonian, very probably zone of *G.* [*A.*] *quadrata*. Specimen marked " W.p." ?Whiteparish, eight miles south-east of Salisbury, Wiltshire. H. P. Blackmore Collection.

D.40681. Zoarial fragment, now unattached. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Locality and collection as for D.28947.

D.40682. Zoarial fragment, now unattached. Horizon, locality and collection as for D.28934.

D.40683–87. Five zoarial fragments, now unattached, the latter with ovicelled zooecia. Horizon, locality and collection as for D.28972.

D.40688–95. Eight zoarial fragments, now unattached. Horizon, locality and collection as for D.40682.

D.40696. Zoarial fragment, now unattached. Horizon, locality and collection as for D.40688.

D.40697. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Section 113 of Gaster, cliff, Rottingdean to Lower Bannings, east of Saltdean Cottages, Sussex.

D.40698–99. Two zoarial fragments, now unattached. Senonian, zone and subzone of *Marsupites*. Section 75 of Gaster, cliff and foreshore east of Brighton at Black Rock, Sussex.

D.40700. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Section 114 of Gaster, cliff, Lower Bannings to Old Nore Point, near Brighton, Sussex.

D.40701. Zoarial fragment, now unattached. Horizon, locality and collection as for D.40700.

D.40702. Zoarial fragment now unattached. Horizon, locality and collection as for D.40697.

D.40703, D.40704–05. Zoarial fragment encrusting a piece of echinoid test and two zoarial fragments now unattached. Horizon, locality and collection as for D.40682.

D.40706. Zoarial fragment, now unattached. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit 87 of Gaster, near cart-track to Newlands Barn, north end of East Hill, Rottingdean, Sussex.

D.40797–802. Six zoarial fragments, now unattached. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 10 of Gaster, pit adjoining Charman Dean Lane, on east side, and west of Pit 9 of Gaster, north of Broadwater and Worthing, Sussex.

D.40803–54. Fifty-two zoarial fragments, now unattached. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 12 of Gaster, large pit north of Pumping Station, top of Waterworks Lane, north-east of " The Warren ", north of Broadwater and Worthing, Sussex.

D.40855. Zoarial fragment, now unattached, partly embedded in small block of chalk. Senonian, zone of *G.* [*A.*] *quadrata*. Pit south of Beech Copse, Michelgrove, Sussex.

D.40856. Zoarial fragment, now unattached. Horizon, locality and collection as for D.28968.

D.40857–59, D.40930. Four zoarial fragments, now unattached. Senonian, zone of *G.* [*A.*] *quadrata.* Large pit about one-third of a mile south-south-east of Salvington Windmill, and north of Hill Cottages, Salvington, Sussex.

D.40946. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.40706.

D.40947. Zoarial fragment encrusting three pieces of echinoid test. Horizon, locality and collection as for D.40697.

D.40948. *Pelmatopora* cf. *gregoryi.* Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.40697.

D.40949. Small zoarial fragment encrusting part of a cheilostome polyzoan. Horizon, locality and collection as for D.28934.

D.40950–51. *Pelmatopora* cf. *gregoryi.* Two zoarial fragments, now unattached. Horizon, locality and collection as for D.28934.

D.40952–53. *Pelmatopora* cf. *gregoryi.* Two zoarial fragments, now unattached. Horizon, locality and collection as for D.40697.

D.40955–67. Thirteen zoarial fragments, now unattached. Horizon, locality and collection as for D.28934.

D.40968–71. Four zoarial fragments, now unattached. Horizon, locality and collection as for D.28953.

D.40972. Zoarial fragment, now unattached. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit 25 of Gaster, small roadside pit, just over half a mile south of Burpham, one-third of a mile north of South Woodleighs Pit (26 of Gaster), west-north-west of Warningcamp Hill, north-east of Arundel, Sussex.

D.40974. Incomplete erect, cylindrical zoarium. Horizon, locality and collection as for D.28934.

D.40975. Zoarial fragment, now unattached. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit 5 of Gaster, locality and collection as for D.28963, see above.

D.40976. Zoarial fragment, now unattached. Horizon, locality and collection as for D.28953.

D.40977–81. Five zoarial fragments, now unattached. Horizon, locality and collection as for D.28947.

D.40982–90. Nine zoarial fragments, now unattached. Horizon, locality and collection as for D.28934.

D.40991–92, D.40993. Two zoarial fragments encrusting pieces of echinoid test, and a zoarial fragment, now unattached. Horizon, locality and collection as for D.28953.

D.40994–41018. Twenty-five zoarial fragments, now unattached. Horizon, locality and collection as for D.28934.

D.41019. Zoarial fragment, now unattached, some zooecia with sealed orifices. Horizon, locality and collection as for D.28934.

D.41020–29. Ten zoarial fragments, now unattached. Horizon, locality and collection as for D.28934.

D.41030–35. Six zoarial fragments, now unattached. Horizon, locality and collection as for D.28953.

D.41041. Zoarial fragment with some ovicelled zooecia, fragment now unattached. Horizon, locality and collection as for D.28934.

D.41043. *Pelmatopora* cf. *gregoryi*. Worn, large zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Section Z of Gaster, Swansbourn Lake Section, Arundel Park, Arun Gap, Sussex.

D.41044. Zoarial fragment, now unattached, very well preserved. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Locality and collection as for D.28963.

D.41045–46. Two zoarial fragments encrusting the same piece of echinoid test. Horizon, locality and collection as for D.40700.

D.41058. Very well preserved, erect, cylindrical zoarial fragment. Horizon, locality and collection as for D.28934.

D.41059. Well-preserved, large, zoarial fragment, now unattached. Horizon, locality and collection as for D.28953.

D.41060–61. Two zoarial fragments encrusting pieces of echinoid test. Horizon, locality and collection as for D.40697.

D.41062. Well-preserved zoarial fragment, now unattached. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Section 142 of Gaster, cliff, Old Nore Point to Inn on west side of entrance to Newhaven Harbour, Sussex.

D.41063. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for D.40697.

OTHER MATERIAL

S.M., B.36120. Lectotype—see above.

21. *Pelmatopora somptingensis* Lang

(Pl. 14, figs. 5, 6; Pl. 15, figs. 1, 2, 4; Text-figs. 95–99)

1906 *non Cribrilina gregoryi* Brydone, pp. 290, 300, text-fig. 13.
1913 *Cribrilina gregoryi* Brydone: Lang, p. 171 [*partim*—D.23963 only].
1916*a* *Pelmatopora somptingensis* Lang, pp. 103, 106.
1916*a* *Pelmatopora danktonensis* Lang, pp. 103, 106.
1919*d* *Pelmatopora somptingensis* Lang: Lang, pp. 214, 221, 224, text-figs. 57–58.
1919*d* *Pelmatopora danktonensis* Lang: Lang, pp. 215, 221.
1921 *Pelmatopora somptingensis* Lang: Lang, p. xci.
1921 *Pelmatopora danktonensis* Lang: Lang, p. xcii.
1922 *Pelmatopora somptingensis* Lang: Lang, p. 300, text-figs. 73*c*, 94.
1922 *Pelmatopora danktonensis* Lang: Lang, p. 309, text-figs. 73*e*, 96.
1924 *Pelmatopora somptingensis* Lang: Gaster, second of three tables opp. p. 110.
1930 *Pelmatopora danktonensis* Lang: Gaster, table opp. p. 340.

HOLOTYPE. D.28762. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *G.* [*A.*] *quadrata*. Sompting, Sussex. T. H. Withers Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with a pair of laterally flattened, distally expanded, enlarged distal oral spines which have a marked tendency to bifurcate.

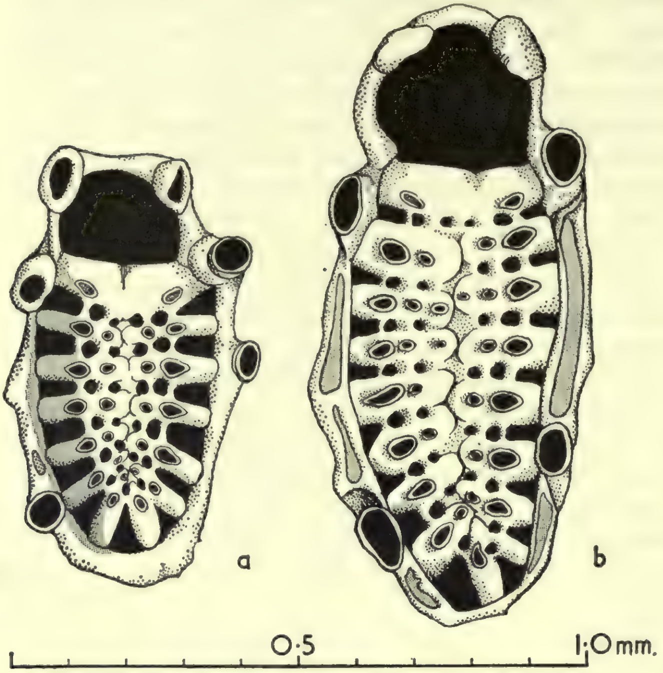
DESCRIPTION. *Zoarium* unilaminar, encrusting, or now unattached. *Adult zooecia* elliptical or with almost parallel sides. *Orifice* wider than high, distally and laterally rounded, with a straight proximal margin, the outline much indented by the pair of enlarged distal oral spines. *Oral spines* 4, only the distal pair visible; they are much enlarged, laterally flattened, expanded distally, and have a marked tendency to bifurcate—the " outer horn " of the bifurcation often considerably produced towards the proximal-lateral margins of the orifice. The unmodified lateral oral spines are always concealed by secondary tissue round the margin of the orifice. *Frontal shield* of variable length, apparently flat. *Costae* 14–22 (often 16 or 17), well spaced and well defined, each with a larger outer and a smaller inner *pelma*, and often with a *pelmatidium* close to the mid-line. *Lateral costal fusions* occur at the levels of the pelmata, producing two paired rows of *intercostal spaces*. *Apertural bar* wide, low, sloping down distally to the orifice and with obscure pelmata. *Gymnocyst* concealed by plentiful *interzooecial secondary tissue* which fills the interzooecial valleys. Slight, shallow, irregularly elongate depressions occur in the surface of the interzooecial tissue.

Avicularia large, prominent, distally pointed and directed, regularly paired, one near each proximal-lateral corner of the orifice. The form of the avicularian aperture is variable; it may be slit-like, as in D.39361, widely oval but pointed distally, oval proximally and slit-like distally, as in D.39343, or very occasionally, with a *transverse bar* dividing the aperture into an approximately semicircular proximal portion and a triangular *rostrum*. The various avicularian apertures are often raised on robust stalks of variable length (Text-fig. 98).

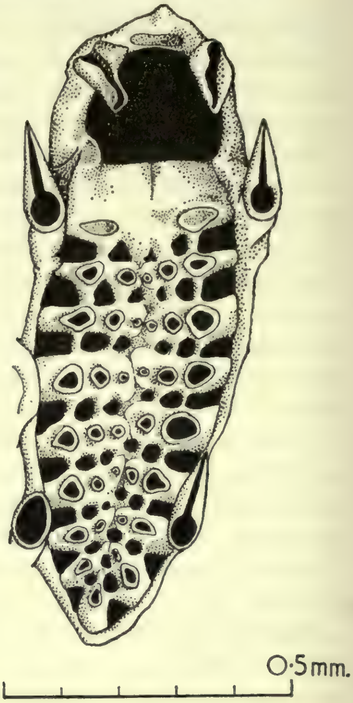
Ovicells apparently endozooecial. In ovicelled zooecia, the space between the enlarged distal oral spines is infilled with secondary calcareous tissue producing a prominent, somewhat pointed distal oral shield.

Young zooecia smaller than the adult and less complex. Very young zooecia close to the ancestrula have typically well-arched frontal shields with somewhat flattened median areas. The enlarged distal oral spines are more peg-like rather than expanded as in the adult zooecia. Costae 10–12, even in the smallest zooecia, each with a pelma about half-way along its length. It is difficult to determine whether pelmatidia are present—possibly they occur very close to the mid-line. Apertural bar relatively very wide. The gymnocyst is possibly revealed in small, deep lacunae in the plentiful interzooecial secondary tissue. Avicularia are apparently already paired in the very young stages of zoarial growth, one on either side of each zooecium, but they are not definitely placed near the proximal-lateral corners of each orifice.

Less young zooecia are larger than those immediately surrounding the ancestrula, but otherwise generally similar, the avicularia tend to be more definitely paired near the proximal-lateral corners of the orifice, and the enlarged distal oral spines are larger with a definite tendency to expand at their distal ends.



95



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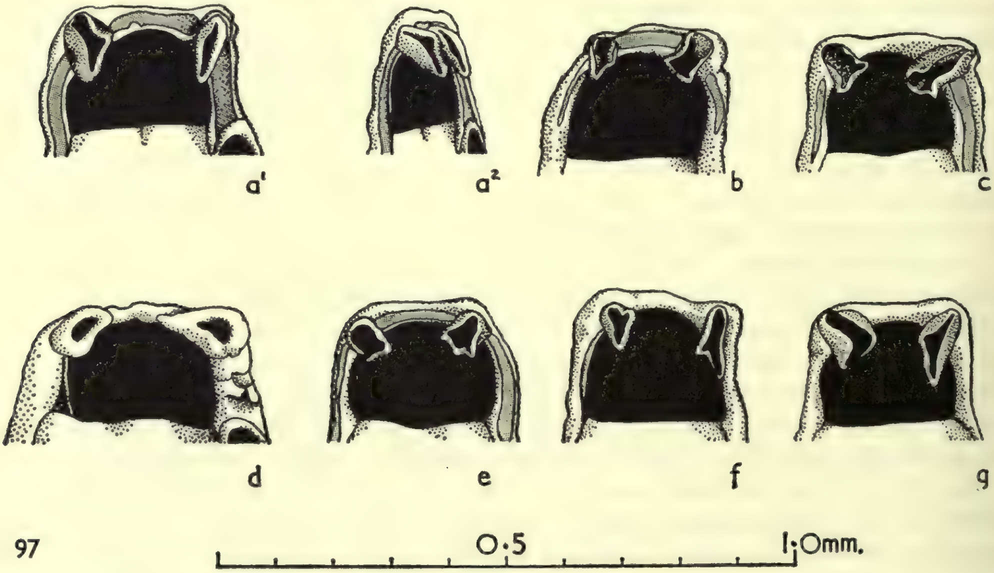

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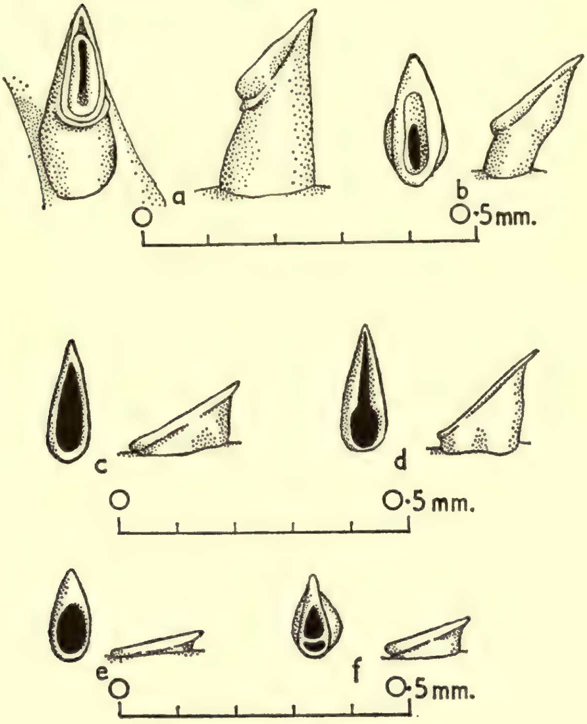
FIGS. 95–97. *Pelmatopora somptingensis* Lang.

(95) D.28747. Paratype. (*a*) Young zooecium and four worn avicularia. (*b*) Adult zooecium and four worn avicularia; the enlarged distal oral spines are very worn.

(96) D.28762. Holotype. Adult zooecium with well-preserved distal oral spines and one worn and three unworn avicularia. The two proximal avicularia belong to adjacent zooecia.

(97) Orifices of seven adult zooecia of several zoaria. The variation in form of the enlarged distal oral spines is due largely to different degrees of wear. (a^{1-2}) D.28762, holotype, front and oblique side views; (*b, f*) D. 39346; (*c, g*) D. 39343; (*d*) D.28762, holotype; (*e*) D.39338.



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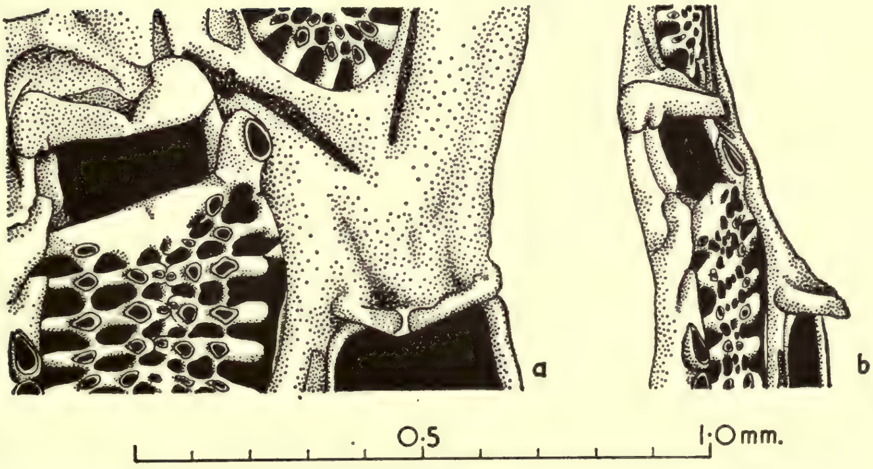


99

FIGS. 98–99. *Pelmatopora somptingensis* Lang.

(98) Unworn avicularia. (*a*, *b*) D.39361 ; (*c*, *d*) D. 39343 ; (*e*, *f*) D. 28770, paratype.

(99) D.28770. Paratype. (*a*) Front view and (*b*) side view of parts of two adult, ovicelled zooecia with shelf-like distal oral shields produced by the infilling of the space between the distal oral spines with secondary calcareous tissue.

MEASUREMENTS. *Adult zooecia* Lz = 1·00 to 1·15 mm.
lz = 0·45 to 0·55 mm.
hr = 0·18 to 0·21 mm.
lr = 0·21 to 0·24 mm.
Avicularia Lz = 0·15 to 0·20 mm.
lz = 0·07 to 0·09 mm.
Young zooecia
(Outer edge of circum-ancestrular area)
Lz = 0·65 to 0·78 mm.
lz = 0·39 to 0·45 mm.
(Very close to the ancestrula)
Lz = 0·50 to 0·54 mm.
lz = 0·33 to 0·35 mm.

REMARKS. The holotype and all available specimens identified by Lang as *P. somptingensis* have been re-examined. *P. danktonensis* Lang is synonymous with *P. somptingensis* Lang. The holotype of *P. danktonensis*, D.23963, has all the features typical of the worn examples of *P. somptingensis*. The range in number of costae in D.23963 is 13–19 ; the enlarged distal oral spines, where preserved, are lengthened distally and are relatively broad, the position and form of the avicularia compares closely with those in *P. somptingensis*, and the stratigraphical distribution is well within the range of *P. somptingensis*.

In *P. somptingensis* the avicularian aperture varies in form as described above. It is significant that the avicularia, where unworn, are raised on robust stalks so that the apertures slope upwards distally and are raised above the general level of the zoarium. They are thus particularly exposed to wear, and may often be reduced to the apparently oval form which the avicularia of most slightly abraded specimens appear to have, and which is almost certainly produced by abrasion wearing down the hollow, oval avicularian stalks (e.g., the worn avicularia shown in Text-fig. 95*a*, *b*).

The enlarged distal oral spines of *P. somptingensis* may show a considerable variety of shape and size, largely dependent on the amount of abrasion they have undergone. Text-fig. 97*a–g* illustrates a series of orifices from several zoaria : the variations in form are due almost entirely to different degrees of wear, but the enlarged distal oral spines all tend to be distally extended and bifurcated, contrasting with the more narrowly elongate and more pointed enlarged distal oral spines of *P. gregoryi*, and with the smaller, peg-like enlarged distal oral spines of *P. marsupitorum*.

The description, given above, of very young zooecia and zooecia at the periphery of the circum-ancestrular area is based primarily on D.28747. Although Lang (1922 : 301) has described its ancestrula, it is not possible to determine its form definitely. The specimen is well preserved, particularly in the circum-ancestrular area, but the smallest visible zooecium is considerably damaged and further obscured by two somewhat larger zooecia which stand up above the general level of the zoarium.

D.29064 is an extremely large, somewhat worn, encrusting zoarium of *P. somptingensis* with at least one abnormal zooecium produced, apparently, by the coalescence of the buds of two adjacent rows of zooecia. It is similar in general form to that figured from D.39301—a specimen of *P. gregoryi.*

A large number of specimens have been assigned to *P. somptingensis*. The species is particularly abundant in the material collected by Gaster from the zone of *G.* [*A.*] *quadrata.*

In paratype D.28770, and in D.39343, ovicelled zooecia with prominent distal oral shields are present. The variations shown by D.39343 in the number of costae in individual zooecia, in the shape of the zooecia, and in the form of the enlarged distal oral spines, are fairly typical of the species as a whole. Well-preserved oral spines and avicularia occur particularly in the following specimens: D.39331, D.39335, D.39338, D.39346, D.39349, D.39350, D.39361, D.39372, D.39377, D.39407, D.39409, and D.39413. The enlarged distal oral spines of D.39377 have an extremely wide bifurcated form which approaches that typical of the distal oral spines of *P. palmata.*

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula* (upper part) into the zone of *G.* [*A.*] *quadrata* (especially abundant in the latter zone).

SPECIMENS. D.28762. Holotype—see above.

D.28101–09, D.28747–61, D.28763–75. Thirty-seven paratypes. Zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 7 of Gaster, Upton Lane (Lambley's Lane), north-west of Sompting, Sussex. [The same locality, horizon and collection as the holotype.]

D.28776–86, D.28788–94, D.28797, D.28979–85. Twenty-five paratypes. Zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 9 of Gaster, eastern pit in lane on eastern side of Charman Dean, north of Broadwater, Sussex. T. H. Withers Collection [except D.28979–85, C. T. A. Gaster Collection].

D.28798–801, D.28988–92. Nine paratypes. Zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 10 of Gaster, western pit in lane on eastern side of Charman Dean, north of Broadwater, Sussex. D.28798–801, T. H. Withers Collection; D.28988–92, C. T. A. Gaster Collection.

D.4338, D.29062. Two zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* East Harham, south of Salisbury. W. Gamble Collection.

D.29056–58. Three zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 8 of Gaster, about half-way between Upton Lane (Lambley's Lane), Sompting, and the lane east of Charman Dean, north of Broadwater, Sussex.

D.39331. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 12 of Gaster, large pit north of Pumping Station, top of Waterworks Lane, north-east of "The Warren", north of Broadwater and Worthing, Sussex.

D.39332–37, D.39465. Seven zoarial fragments. Horizon, locality and collection as for D.28798.

D.39338, D.39342–43, D.39345–47, D.39349–50, D.39353–54, D.39358, D.39361–62, D.39364–65, D.39367, D.39409, D.39466, D.40054–56. Twenty-one zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 15 of Gaster, large pit about one-third of a mile south-east of Salvington Windmill, and north of Hill Cottages, Salvington, Sussex.

D.23963. Holotype of *P. danktonensis* Lang. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit 5 of Gaster, pit in Dankton Lane, north of Sompting Church, north-east of Worthing, Sussex. W. D. Lang Collection.

D.29862. Zoarial fragment labelled by Lang "*P. danktonensis*". Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Cliffs, west of Broadwater and Castle Hill, Newhaven, Sussex.

D.29877–78, D.29864. Three zoarial fragments, the last labelled by Lang "*P. danktonensis*". Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula* (upper part). Pit 2 of Gaster, pit by reservoir, near Hill Barn, North Lancing, Sussex.

D.29863. Zoarial fragment labelled by Lang "*P. danktonensis*". Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Pit 4 of Gaster, pit west of Boundstone Lane, south of Lancing Ring, north-east of Worthing, Sussex.

D.39372, D.39374–75, D.39377, D.39380–81*a*, *b*, D.39384–85, D.39467–68. Fragments of eleven zoaria. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 20 of Gaster, lower pit on Patching Hill, north of St. John's Church, Patching, Sussex.

D.39391, D.39469. Two zoarial fragments encrusting pieces of echinoid test. Horizon, locality and collection as for D.28101.

D.39394, D.39470–72. Four zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 44 of Gaster, by Mile Oak Road, about one-third of a mile north-east of Windmill Inn, Southwick, one furlong north of Upper Shoreham Road, Sussex.

D.39395–96, D.40129, D.40131. Four zoarial fragments. Horizon, locality and collection as for D.29056.

D.39397, D.39473–75. Four zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 18 of Gaster, Old Lime Kiln, north-west corner of Munery's Copse, west of Pit 17 of Gaster, and east end of Clapham Wood, Sussex.

D.39402, D.39476–78, D.40067–73, D.40087–97, D.40109–10, D.40111–24, D.40132. Thirty-nine zoarial fragments. Horizon, locality and collection as for D.28776.

D.39404, D.39479, D.40050–53. Six zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 26 of Gaster, South Woodleighs Pit, east of gravel pit, north-east of Woodleighs Lodge, about half a mile west of pit 24 of Gaster, Warningcamp, north-east of Arundel, Sussex.

D.39407. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata*. From material labelled "Pits 17, 18, 19, 24 and 32" of Gaster [all in the zone of *G.* [*A.*] *quadrata*].

D.39411. Zoarial fragment with some ovicelled zooecia. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 35 of Gaster, small pit, north of Rake Mead Plantation, Church Hill Shaw, about half a mile north-west of Roger's Farm, and west of South Park, just above 400 ft. contour, Findon, Sussex.

D.39413. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata.* From material labelled " Pits 8, 11, 15, 16, 17, and 23 " of Gaster. [All in the zone of *G.* [*A.*] *quadrata.*]

D.40074–78, D.40104, D.40081–86, D.40079–80. Fourteen zoarial fragments. Horizon locality and collection as for D.28101.

D.40106–07. Two zoarial fragments. Horizon, locality and collection as for D.28101.

D.40098–103, D.40105, D.40125–28, D.40130, D.39450–53. Sixteen zoarial fragments. Horizon, locality and collection as for D.28798. D.39450–53, T. H. Withers Collection.

D.40108. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata.* Pit 23 of Gaster, near Angmering Park Cottages, Angmering, Sussex.

D.39435–49. Fifteen zoarial fragments. Horizon and locality as for D.28101. T. H. Withers Collection.

D.29064. Zoarial fragment. Senonian, zone uncertain, very probably zone of *G.* [*A.*] *quadrata.* South of England. F. H. Butler Collection.

D.39454–63. Ten zoarial fragments. Horizon, locality and collection as for D.29877.

D.39464. Zoarial fragment. Horizon, locality and collection as for D.28101.

D.29876. Zoarial fragment. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit by roadside between Burpham and Arundel, and west-north-west of Warningcamp Hill, Sussex.

D.40718–19. Two zoarial fragments encrusting pieces of echinoid test. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Locality as for D.29877.

D.40720. Zoarial fragment, now unattached. Horizon and locality as for D.28101.

D.40721. Zoarial fragment, now unattached. Horizon and locality as for D.28776.

D.40748–56. Nine zoarial fragments, now unattached. Horizon, locality and collection as for D.28798.

D.40757–85. Twenty-nine zoarial fragments, now unattached. Horizon, locality and collection as for D.29056.

D.40786–88. Three zoarial fragments now unattached. Horizon, locality and collection as for D.28798.

D.40789–96. Eight zoarial fragments, now unattached. Horizon, locality and collection as for D.39331.

D.40954. *Pelmatopora* cf. *somptingensis.* Zoarial fragment, now unattached. Senonian, zone of *O. pilula,* subzone of *E. scutata* var. *cincta.* Pit 25 of Gaster, small roadside pit, just over half a mile south of Burpham, one-third of a mile north of Pit 26 of Gaster, west-north-west of Warningcamp Hill, north-east of Arundel, Sussex.

22. *Pelmatopora palmata* Lang

(Pl. 15, figs. 3, 5, 6; Text-figs. 100–102)

1916*a* *Pelmatopora palmata* Lang, pp. 103, 107.
1916*a* *Pelmatopora damicornis* Lang, pp. 103, 107.
1916*a* *Pelmatopora* (*Cribrilina*) *gregoryi* (Brydone): Lang, p. 106 [*partim*—D.8009, D.28537, D.21169 only].
1919*d* *Pelmatopora palmata* Lang: Lang, pp. 199, 214, 221, text-figs. 12–14, 59, 60.
1919*d* *Pelmatopora damicornis* Lang: Lang, pp. 215, 221.
1921 *Pelmatopora palmata* Lang: Lang, p. xci.
1921 *Pelmatopora damicornis* Lang: Lang, p. xci.
1922 *Pelmatopora palmata* Lang: Lang, p. 306, pl. 6, fig. 7; text-figs. 73*d*, 96.
1922 *Pelmatopora damicornis* Lang: Lang, p. 307.
1922 *Pelmatopora gregoryi* (Brydone): Lang, p. 304 [*partim*—D.8009, D.28537, D.21169 only].
1924 *Pelmatopora palmata* Lang: Gaster, second of three tables opp. p. 110.
1930 *Pelmatopora palmata* Lang: Gaster, table opp. p. 340.

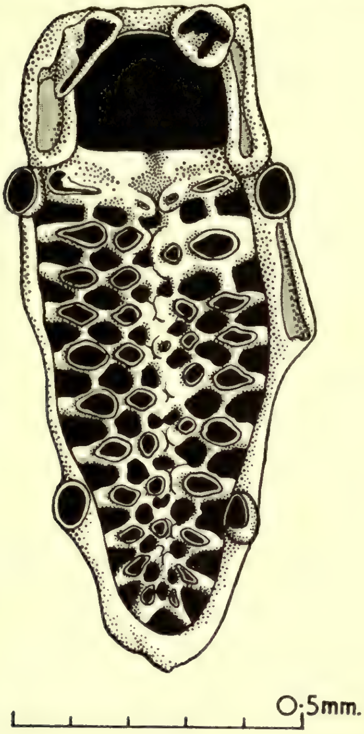
HOLOTYPE. D.8010. Zoarial fragment, now unattached, Senonian, zone of *G.* [*A.*] *quadrata*. Winchester, Hampshire. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Pelmatopora* with a pair of enlarged distal oral spines which are very broad distally and distinctly bilobed.

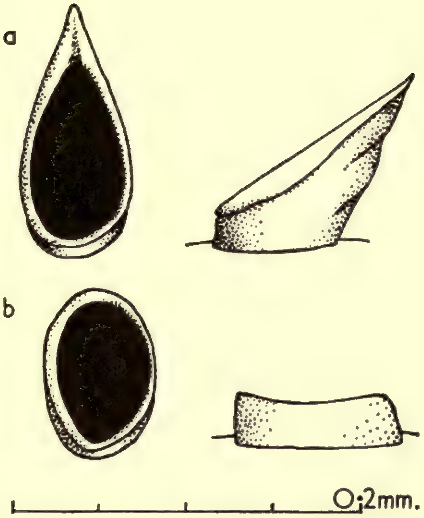
DESCRIPTION. *Zoarium* uni- or bilaminar, encrusting or now unattached. *Zooecia* elliptical, the sides tending to be parallel. *Orifice* wider than high, distally and laterally rounded, with a straight proximal margin, its outline very much indented by the pair of enlarged distal oral spines. *Oral spines* 4 only the distal pair visible; these are much enlarged, distally expanded and distinctly bilobed. The unmodified pair of lateral oral spines is always concealed by secondary tissue accumulated round the margin of the orifice. *Frontal shield* of variable length, apparently fairly flat. *Costae* 16–20 (often 18 or 19), well defined, each with a larger outer and a smaller inner *pelma*, and usually with a *pelmatidium* near the mid-line. *Lateral costal fusions* arise at the levels of the pelmata producing two paired rows of *intercostal spaces*. *Apertural* bar wide, low, with obscure pelmata; the apertural bar slopes down slightly towards the proximal edge of the orifice. *Gymnocyst* entirely concealed by *interzooecial secondary tissue* which fills the interzooecial valleys and which contains irregularly elongate shallow depressions.

Avicularia prominent, large, distally pointed and directed, regularly paired, one near each proximal-lateral corner of the orifice. Well-preserved avicularia lack transverse bars, the aperture is semicircular proximally with a distally pointed *rostrum*, the apertures of many avicularia are raised on stout stalks above the general level of the zoarium. *Ovicells* not seen.

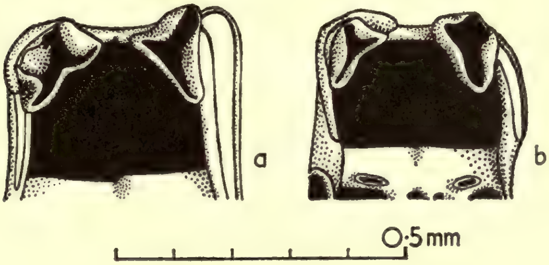
MEASUREMENTS. *Zooecia* Lz = 1·00 to 1·25 mm.
lz = 0·42 to 0·50 mm.
hr = 0·18 mm.
lr = 0·21 mm.
Avicularia Lz = 0·15 mm.
lz = 0·06 mm.



100



102



101

FIGS. 100–102. *Pelmatopora palmata* Lang.

(100) D.8010. Holotype. Adult zooecium and four worn avicularia; those near the proximal end belong to adjacent zooecia. The distal oral spines are typically flat and bilobed, that on the right is worn obliquely.

(101) D.8010. Holotype. Orifices of two adult zooecia. (*a*) markedly flat, bilobed distal oral spines, that on the right is worn; (*b*) both distal oral spines are worn obliquely.

(102) D.8010. Holotype. Avicularia. (*a*) Unworn, (*b*) worn—the oval form is a cross-section of the avicularian stalk.

Remarks. Lang (1922 : 305) interpreted *P. gregoryi* (Brydone) from Brydone's 1906 description and figure. Unfortunately these were not sufficiently clear to show the nature of the enlarged distal oral spines, and Lang supposed *P. gregoryi* to be similar to *P. damicornis* in these respects. He maintained the three species (*P. gregoryi*, *P. damicornis* and *P. palmata*) as separate solely on supposed differences in zoarial growth habit. However, it has been shown that the enlarged distal oral spines of the lectotype of *P. gregoryi*, S.M., B.36120, as well as other zooecial characters, are different from those of *P. palmata*. The latter is thus retained as a separate species, but is regarded as synonymous with *P. damicornis*. The supposed differences in zoarial growth habit of *P. palmata* and *P. damicornis* are very uncertain, and the two species are otherwise morphologically alike.

D.8009, D.28537 and D.21169, labelled by Lang " *Pelmatopora* [*Cribrilina*] *gregoryi* (Brydone) ", are also referred to *P. palmata* Lang. D.8009 and D.28537 are somewhat worn, but appear to have distally expanded, bilobed distal oral spines, and are thus placed in *P. palmata* with a query. D.21169 is better preserved and is placed in *P. palmata* with certainty. D.20204, holotype of *P. damicornis* Lang, is well preserved and may be definitely assigned to *P. palmata*.

It may be significant that there is relatively little material which can definitely be placed in *P. palmata*. This is possibly explained by difficulties imposed by poor preservation, particularly by wear of the enlarged distal oral spines. It has, however, been noted that worn bilobed oral spines differ in form from worn elongate oral spines such as occur in *P. gregoryi*. Where wear has reduced oral spines it is thus possible to differentiate between bilobed and elongate types, but the identification must also rest largely on other zooecial characters, such as zooecial size, range in number of costae, type and amount of interzooecial tissue and form and distribution of avicularia.

D.39355 and D.39356 have especially well-preserved enlarged distal oral spines typical of *P. palmata*.

Stratigraphical distribution. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta* to zone of *G.* [*A.*] *quadrata*.

Specimens. D.8010. Holotype—see above. [The specimen is labelled " Idiotype of *P. gregoryi* (Brydone) ".]

D.28971. Paratype. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 8 of Gaster, between Upton Lane (Lambley's Lane), Sompting, and lane east of Charman Dean, north of Broadwater, Worthing, Sussex.

D.20204. Holotype of *P. damicornis* Lang. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata*. Seaford, Sussex. Collection unspecified.

?D.8009. Large fragment of a worn zoarium. Labelled by Lang " *Pelmatopora gregoryi* (Brydone). Idiotype ". Senonian, zone of *G.* [*A.*] *quadrata*. Sussex Coast. R. M. Brydone Collection.

?D.28537. Three fragments of the same zoarium. Labelled as for D.8009. Senonian, horizon unspecified, probably zone of *G.* [*A.*] *quadrata*. Southern England. F. H. Butler Collection.

D.21169. Zoarial fragment. Labelled as for D.8009. Senonian, zone of *G.* [*A.*]

quadrata. Southampton Waterworks Pit, Otterbourne, south of Winchester, Hampshire. L. Treacher Collection.

D.28865. Zoarial fragment. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *cincta*. Pit on East Hill, Rottingdean, east of Brighton, Sussex.

D.39339, D.39355–56. Three zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 15 of Gaster, large pit about one-third of a mile south-south-east of Salvington Windmill, and north of Hill Cottages, Salvington, Sussex.

D.39370, D.39378. Two zoarial fragments. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 20 of Gaster, lower pit on Patching Hill, north of St. John's Church, just above the 200 ft. contour, Patching, Sussex.

D.39410. Zoarial fragment. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 35 of Gaster, small pit north of Rake Mead Plantation, Church Hill Shaw, about half a mile north-west of Rogers Farm, and west of South Park, just above the 400 ft. contour, Findon, Sussex.

PELMATOPORA sp.

(Pl. 15, fig. 7)

SPECIMEN. D.39330. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Pit 105 of Rowe. White Pit Lane, Newport, Isle of Wight.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Zooecia* elongate-elliptical with somewhat parallel sides. *Orifice* wider than high, distally and laterally rounded, with a straight proximal margin, its outline indented by two worn, enlarged distal oral spines. Only the distal pair of *oral spines* is visible, and only their distinctly rounded bases are preserved; one enlarged oral spine is apparently hollow. Unmodified lateral oral spine-bases, if present, are concealed by secondary tissue. *Frontal shield* of variable length. *Costae* 20–24 (often 22), well defined, each with a fairly prominent *pelma* near its outer end, a second smaller pelma about half-way along its length, and a *pelmatidium*, often obscure, near the mid-line. *Lateral costal fusions* arise at the level of the pelmata producing two paired rows of *intercostal spaces*; an additional irregularly developed row of small intercostal spaces may occur very close to the mid-line. The outermost intercostal spaces are slot-like. *Apertural bar* wide, flat, sloping down towards the proximal margin of the orifice. *Gymnocyst* entirely concealed by *interzooecial secondary tissue*, which fills the interzooecial valleys and which contains irregular, elongate, shallow *lacunae*.

Avicularia either oval or elongate and distally pointed. In the specimen, all avicularia are worn. There is, however, a strong tendency for the avicularia to be arranged in pairs, one near each proximal-lateral corner of the orifice. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 1·24 to 1·50 mm.
lz = 0·42 to 0·50 mm.
hr = 0·15 to 0·18 mm.
lr = 0·18 to 0·21 mm.
Avicularia Not measurable.

REMARKS. Lang has stated that *Pelmatopora* does not range above the zone of *G.* [*A.*] *quadrata*. However, D.39330 was collected from Pit 105 of Rowe, which was placed by him (1908 : 280) in the zone of *B. mucronata* " beyond doubt ". Recent collecting neither confirms nor disproves Rowe's suggested horizon for his Pit 105.

Some features of D.39330 are unlike any seen in the other known species of *Pelmatopora*; the large size of the zooecia and the large number of costae are particularly unusual. One zooecium with 28 costae is distorted proximally and is regarded as abnormal, the usual range in the specimen being 20–24. The specimen obviously belongs to the group of *Pelmatopora* species which possess enlarged distal oral spines, and it is very probable that its enlarged oral spines are not of the expanded bilobed type but rather of the elongate, outwardly curving form, with rounded bases, such as are developed in *P. gregoryi*.

Although the specimen is unlike any known species of *Pelmatopora*, it is not advisable to erect a new species on a single somewhat worn specimen, and diagnosis must depend on better preserved material. The specimen is important as the only definite *Pelmatopora* from the zone of *B. mucronata*.

Although Voigt (1925*b*; 1930) has assigned species from the zone of *B. mucronata* and higher horizons to *Pelmatopora*, these may not be correctly placed in that genus. An exceptional occurrence of *Pelmatopora* in the Danian is noted in the remarks on *P. daniensis* Voigt (p. 202).

SPECIES OF UNCERTAIN SYSTEMATIC POSITION PREVIOUSLY ASSIGNED TO *PELMATOPORA*

(1) ***Pelmatopora incerta*** Voigt

1925*b* *Pelmatopora incerta* Voigt, pp. 99, 100, pl. 3, figs. 9, 10; text-fig. 1.
1930 *Pelmatopora incerta* Voigt: Voigt, pp. 515, 561, pl. 31, fig. 15 [part of the same zoarium figured by Voigt, 1925*b*, pl. 3, fig. 9].
1939 *Pelmatopora incerta* Voigt: Voigt, p. 93, text-fig. 4*a* [copy of Voigt, 1925*b*, text-fig. 1].

DESCRIPTION. [Based on Voigt's descriptions and figures.] *Zoarium* unilaminar, encrusting. *Zooecia* about two-thirds as wide as long. *Orifice* about as long as wide, distally and laterally rounded, with a straight proximal margin, and with proximal-lateral " slits ". *Oral spine-bases* 4, *frontal shield* flatly arched. *Costae* about 20, closely spaced, " fused " only in the mid-line, each with a number of *pelmatidia* (the outermost and the innermost pelmatidia appear to be better developed than the intervening ones). Individual costae taper towards their inner ends and have slightly curved margins (? = the slightly crenulate outlines shown in Voigt's text-figure). *Lateral costal fusions* possibly present. The costae meet and fuse in the mid-line, producing a slight median ridge, or, as in at least one zooecium figured by Voigt, there is a flat median area. *Gymnocyst* well exposed, especially proximally to the frontal shield. *Interzooecial secondary tissue* apparently absent.

Avicularia apparently rare, elongate, oval (their form is not apparent from the photographs). *Ovicells* not seen.

REMARKS. Voigt has suggested that the species belongs to the group of " primitive ", less complex *Pelmatopora* species in which the costae are fused only in the mid-line. Although this is apparently so in several of the zooecia figured by Voigt, each costa also has a row of pelmata or pelmatidia—a condition found in the later, more complex species of *Pelmatopora*. Also, in the earlier forms of *Pelmatopora*, the costae are characterized by single, large pelmata developed near the mid-line of the frontal shield, or surrounding the median area of fusion when this is present. In *incerta* the larger pelmata or pelmatidia are distinctly at the extreme outer ends of the costae. The avicularia, described by Voigt as rare and elongate oval, are not discernible in the photographs. The stylized text-figure shows a single avicularium which is directed proximally and constricted laterally so that it is partly divided into a smaller semicircular portion and a distal area which is elongate-oval. This type of avicularium is unknown in other species of *Pelmatopora*.

In the absence of actual material it is undesirable to attempt to decide the definite systematic position of a species known only from inadequate photographs and descriptions. However, *incerta* is very probably not a *Pelmatopora*.

STRATIGRAPHICAL DISTRIBUTION. " Ob. Senongeschiebe ", Köthen.

(2) ***Pelmatopara grandiporosa*** Voigt

1930 *Pelmatopora grandiporosa* Voigt, pp. 514, 561, pl. 31, figs. 13, 14.

DESCRIPTION. [Based on Voigt's description and figures.] *Zoarium* unilaminar, encrusting. *Zooecia* about twice as long as wide. *Orifice* large, distally and laterally rounded, with a straight proximal margin. Number and form of *oral spines* unknown. *Frontal shield* apparently fairly flat, but curving down steeply at the margins to meet the gymnocyst. *Costae* about 10, very wide, very irregularly arranged, each with a large, oval *pelma* at the outer end. *Interzooecial secondary tissue* probably abundant.

Avicularia not distinct in the photographs, but, according to Voigt, many small avicularia occur between the zooecia.

REMARKS. From the photographs it is not possible to place this species in *Pelmatopora*. Voigt has suggested that the irregular arrangement of the few,very thick costae distinguishes the species from all known species of *Pelmatopora*, but this irregular arrangement of the costae, their coarseness, and the numerous interzooecial avicularia which Voigt mentioned, all contrast with the generally settled more complex pattern of *Pelmatopora* at the horizon involved. The placing of the species as a *Pelmatopora* is thus very uncertain, and, in the absence of actual material, it may not be described with certainty beyond " cribrimorph of the Pelmatoporidae ".

STRATIGRAPHICAL DISTRIBUTION. Granulatensenon. Gt. Bülten.

(3) ***Pelmatopora*** sp.

1930 *Pelmatopora* sp., Voigt, pp. 514, 561, pl. 31, fig. 12.

REMARKS. Voigt described the zoarium as " free ", bilaminar, with zooecia of Lz = 0·75 to 0·80 mm., and with frontal shield with 10–13 costae, he could not identify it with any of Lang's species of *Pelmatopora*.

The photograph of the specimen is small, but apparently shows at least one lateral costal fusion arising between the inner ends of the costae near a narrow median area.

From the description and photograph alone it seems very uncertain that the specimen should be placed in *Pelmatopora*.

STRATIGRAPHICAL DISTRIBUTION. " Granulatensenon ". Gt. Bülten.

(4) ***Pelmatopora daniensis*** (Voigt)

1925*b* *Pelmatopora daniensis* Voigt, pp. 99, 100, pl. 3, figs. 4–6 ; text-fig. 2.
1930 *Pelmatopora daniensis* Voigt : Voigt, pp. 514, 561, pl. 31, fig. 11.

DESCRIPTION. (Based on Voigt's figures.) *Zoarium* apparently unilaminar, erect. *Zooecia* elongate-oval. *Orifice* wider than high, evenly rounded distally and laterally, proximal margin straight. *Oral spine-bases* 4, slightly enlarged, unmodified. *Frontal-shield* fairly well arched. *Costae* 20–24, each with 4 or 5 *lateral costal fusions* and *pelmatidia* ; *outermost intercostal* spaces distinct. *Apertural bar* narrow, form obscure. *Gymnocyst* hardly visible ; no *interzooecial secondary tissue*.

Avicularia proximally directed, large, elongate-oval, somewhat pointed, a prominent *transverse bar* divides a small semicircular proximal portion from a longer, bluntly triangular *rostrum*. Avicularia one-quarter to one-third as long as the zooecia they accompany, irregularly distributed, apparently comparatively rare. *Ovicells* not seen.

MEASUREMENTS. (According to Voigt, 1925*b*, p. 101.)

Zooecia Lz = 0·75 to 1·05 mm.
lz = 0·36 to 0·44 mm.
Avicularia Lz = 0·21 to 0·24 mm.
lz = 0·08 to 0·12 mm.

REMARKS. The shape of the orifice, the nature of the frontal shield, and particularly the form of the avicularia, distinguish this species from other species of *Pelmatopora*, but the characters are reminiscent in some ways of *Castanopora*.

It is difficult to be certain that the specimens which Voigt (1925 : 99, 100, pl. 3, figs. 4–6) assigned to *Pelmatopora daniensis* should be placed definitely in that genus. However, Mr. Ole Berthelsen has very kindly shown me a single specimen from the Upper Danian of Herfølge, Seeland, which differs in some respects from Voigt's description and figures, but which is undoubtedly a *Pelmatopora*. The occurrence of this genus at this horizon is exceptional.

Voigt himself compared his species (1925*b* : 101) with *Repteschareila radiata* d'Orbigny (1852, pl. 716, figs. 4–6), commenting " Eine gewisse Ähnlichkeit mit unserer Form zeigt *Repteschareila radiata* d'Orb., ist jedoch von ihr durch das inkrustierende Zoarium und durch weniger zahlreiche (16–18) aus etwa je 7–8 Poren gebildete Punktreihen verschieden ". *Repteschareila radiata* d'Orbigny was assigned by Lang (1922 : 187) to *Rhiniopora*. As Voigt stated, it is an encrusting form with fewer costae and slightly fewer intercostal spaces than *daniensis*. It is also possible that *Repteschareila radiata* lacks avicularia.

The horizon of d'Orbigny's material is Campanian and Santonian of Meudon and

Saintes, France, whilst Voigt's specimen is of Danian age from Cöthen. On morphological and stratigraphical features the two are maintained as separate.

STRATIGRAPHICAL DISTRIBUTION. Danian.

Genus ***CASTANOPORA*** Lang

1851	*Cellepora* (? *Dermatopora*) : von Hagenow, p. 99, pl. 10, fig. 19.
1851	*Escharipora* d'Orbigny, pls. 603, 684–687, 700, 703 [*partim*].
?1852	*Repteschareila* d'Orbigny, pls. 604, 715–716 [*partim*].
1852	*Repteschanipora* d'Orbigny, pls. 719, 720 [*partim*].
1852	*Escharipora* : d'Orbigny, p. 221 [*partim*].
?1853	*Repteschareila* : d'Orbigny, p. 464 [*partim*].
?1854	*Repteschareila* : d'Orbigny, p. 1097 [*partim*].
1854	*Escharipora* : d'Orbigny, p. 1097 [*partim*].
?1854	*Repteschanipora* : d'Orbingy, p. 1098 [*partim*].
1865	*Escharipora* : Ubaghs, p. 51.
1887	*Cribrilina* : Marsson, p. 96 [*partim*].
1894	*Membranipora* : Gregory, p. 62.
1896	*Membranipora* : Gregory, p. 212.
?1900*b*	*Repteschanipora* : Canu, p. 457 [*partim*].
?1900*b*	*Cribrilina* : Canu, p. 445 [*partim*].
1906	*Cribrilina* : Brydone, pp. 296–298 [*partim*].
1907	*Cribrilina* : Levinsen, pp. 155–156.
1913	*Cribrilina* : Brydone, pp. 436–438 [*partim*].
1916*a*	*Rhiniopora* Lang, pp. 93, 96–97.
1916*a*	*Castanopora* Lang, pp. 93–96.
1917	*Rhiniopora* : Lang, p. 172.
1919*c*	*Castanopora* : Lang, p. 105, footnote.
1922	*Rhiniopora* : Lang, p. 180.
1922	*Castanopora* : Lang, p. 202.
1923	*Rhiniopora* : Waters, pp. 548, 551.
1923	*Castanopora* : Waters, pp. 548, 551, 558–560.
1925	*Cribrilina* : Levinsen, p. 375 [*partim*].
?1925	*Barroisina* : Levinsen, p. 384 [*partim*].
1925*c*	*Cribrilina* : Voigt, p. 176 [*partim—C. asperula* only].
1927	*Cribrilina* : Voigt, p. 102 [*partim*].
?1927	*Barroisina* : Voigt, p. 102 [*partim*].
1927	*Rhiniopora* : Canu & Bassler, p. 37.
1927	*Castanopora* : Canu & Bassler, p. 25.
1929	*Castanopora* : Lang, pp. 438, 439.
1929	*Rhiniopora* : Lang, pp. 438, 439.
1930	*Rhiniopora* : Voigt, pp. 510, 511, 551, 561.
1930	*Castanopora* : Voigt, pp. 512, 513, 551, 561.
1935	*Castanopora* : Bassler, pp. 31, 65.
1935	*Rhiniopora* : Bassler, pp. 31, 190.
1953	*Castanopora* : Bassler, p. G192.
1953	*Rhiniopora* : Bassler, p. G193.
1953	*Rhiniopora* : Illies, p. 76.
1958	*Rhiniopora* : Butler & Cheetham, p. 1154.

TYPE SPECIES. (By original designation.) *Castanopora castanea* Lang, 1916*a* : 95. Senonian, " zone of *B. mucronata* ", probably boreal Maastrichtian, Rügen.

EMENDED DIAGNOSIS. Pelmatoporinae with numerous costae and numerous pelmata or pelmatidia and lateral costal fusions ; no secondary orifice ; no tertiary front wall, avicularia large, variously directed, of one, two or three kinds, or occasionally none.

REMARKS. Lang established the genera *Castanopora* and *Rhiniopora*, which I consider synonymous, to distinguish between the larger forms of Castanoporinae [here synonymous with the Pelmatoporinae] which lack secondary orifices and tertiary front walls. *Castanopora* was briefly diagnosed (Lang, 1916*a* : 93) as having " avicularia of two kinds, (1) directed distally and (2) directed proximally (the latter kind may be very rare or absent) ", while *Rhiniopora* was distinguished by its avicularia which " (if present) [are] of one kind only, proximally directed ".

In his subsequent expansion of these definitions (1922 : 181, 203) Lang diagnosed the two genera as follows : *Rhiniopora*—" Large Castanoporinae with numerous costae ; with no secondary [= tertiary] front-wall and no secondary aperture ; aviculoecia dimorphic, monomorphic, or none ; when dimorphic, some aviculoecia have long rostra, others pointed (but comparatively short) rostra, the former variously directed, the latter (? always) proximally directed ; when monomorphic, the aviculoecia are always of the latter type ". *Castanopora*—" Large Castanoporinae with numerous costae, no tertiary front-wall and no secondary aperture ; paired, distally directed aviculoecia, having apertures with elongate pointed rostra, are present, and some species have proximally-directed aviculoecia also, with short rostra ".

Lang thus distinguished between *Rhiniopora* and *Castanopora* solely on the form, orientation and kinds of avicularia present. He summarized his general conclusions (1922 : 156) and stated " In both genera the early species possess both long and short aviculoecia, but in *Rhiniopora* they are all variously and on the whole proximally directed, while in *Castanopora* two of the longer aviculoecia, situated more-or-less symmetrically one on each side of each aperture, are distally directed. *Rhiniopora* soon loses the longer aviculoecia and gradually tends to lose the shorter ones as well, while *Castanopora* retains the distally-directed ones and likewise gradually loses the aviculoecia with shorter apertures ".

Waters (1923 : 548) commented on the close similarity of some Cretaceous cribrimorphs with Recent European cribriline genera and stated "—in fact, it almost seems as if some of the Cretaceous forms might be considered varieties of our recent species, though rather larger ; and for the zoologist, the genera *Castanopora* and *Rhiniopora*, separated on slight grounds, are the most interesting (even if the names are dropped) as being represented in the living fauna ". Later (p. 551) Waters states "—the avicularia are given an important place and, like the other characters, must be carefully studied, but we may well remember that in recent Cheilostomatous forms there are not only genera, but species, which sometimes have avicularia, sometimes none. Sometimes, when Lang speaks of dimorphic avicularia, there seems no difference except size . . . Judging from recent forms it would seem natural to say that avicularian characters have been used for the fossil genera where they have not more than specific value, even if that, and in recent species there is very great variation ".

Re-examination of all the available material assigned by Lang to *Rhiniopora* and *Castanopora* makes it difficult to confirm his separation of the genera. Variations in the form, position and orientation of the avicularia are insufficient for such a purpose. But these variations, in conjunction with other characters, are here used to distinguish species. Also, several of the original species which Lang placed in *Rhiniopora* appear to be synonymous, and the same applies to several species originally placed in *Castanopora*.

In the one species which has three kinds of avicularia there are a constantly paired, distally directed and pointed form and two unpaired proximally directed forms, the one sporadic and the other constantly placed just distal to each orifice. In species with two types of avicularia both types are not present in all zooecia ; the most frequently occurring form is usually paired, distally directed and pointed, or occasionally spatulate, the less frequent form is unpaired, rounded, probably due to wear, or pointed, proximally directed and sporadic. Species with only one kind of avicularium also occur—avicularia of this type are frequently paired, pointed and either all distally or all proximally directed ; or occasionally single, almost rounded and sporadic. Very occasionally avicularia may be absent.

I retain the name *Castanopora*, rather than *Rhiniopora*, for the revised genus, and thus the type-species is *Castanopora castanea* Lang.

STRATIGRAPHICAL DISTRIBUTION. Senonian—zone of *Marsupites* to Danian. Canu & Bassler (1933 : 53, 54) assigned two species from the Vincentown Limesand to *Rhiniopora*, thus extending the upward range of the genus into the Palaeocene.[1]

KEY TO THE SPECIES OF *CASTANOPORA*

(I) Zoarium encrusting or erect, uni- or bilaminar.
  (A) *Castanopora* with three types of avicularia . . . 1. ***C. armata*** sp. nov.
  (B) *Castanopora* with two types of avicularia.
    (1) 28–34 costae ; avicularia distally directed, unpaired, very large, rounded, widely spatulate ; a more frequent, proximally directed, small, rounded form also present . . . . . . 2. ***C. labiata*** (Levinsen)
    (2) 16–23 costae.
      (*a*) 4 (less often 3) lateral costal fusions on each costa ; avicularia distally directed, frequently paired, very elongate, sharply pointed ; a proximally directed, shorter, pointed form also present 3. ***C. retrorsa*** Lang
      (*b*) 4-8 (often 6–7 lateral costal fusions on each costa).
        (i) 4 oral spines only ; orifice wider than high ; avicularia distally directed ; frequently paired, elongate, pointed ; an occasional probably proximally directed, rounded sporadic form also present 4. ***C. castanea*** Lang
        (ii) 4 (occasionally 5) oral spines ; orifice slightly wider than high or as wide as high ; avicularia distally directed, elongate, pointed, constantly paired near orifice ; a less frequent, proximally directed, elongate pointed, sporadic form also present 5. ***C. dibleyi*** (Brydone)
        (iii) 5 or 6 oral spines ; avicularia possibly proximally directed, paired near orifice ; an occasional, proximally directed, elongate, pointed, sporadic form also present . . . 6. ***C. guascoi*** (Ubaghs)

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[1] The age of the Vincentown Limesand has been established as Palaeocene by (Loeblich & Tappan, 1957).

(C) *Castanopora* with one type of avicularium.
  (1) Zooecia small, Lz = 0·26 to 0·34 mm., lz = 0·17 to 0·27 mm., hr = 0·04 to 0·07 mm., lr = 0·06 to 0·09 mm. . 7. ***C. spooneri*** (Butler & Cheetham)
  (2) Zooecia larger, Lz more than 0·75 mm., lz more than 0·36 mm., hr more than 0·15 mm., lr more than 0·15 mm.
    (*a*) Orifice wider than high.
      (i) 5–6 oral spines ; 26–30 costae, each with about 9 lateral costal fusions ; avicularia distally directed, paired near orifice, elongate, pointed . . . . . . 8. ***C. multicostata*** (Voigt)
      (ii) 6 oral spines only ; costae with 8 lateral costal fusions ; 25–30 costae ; avicularia rounded, fairly frequent, sporadic 9. ***C. jurassica*** (Gregory)
    (*b*) Orifice higher than wide or height approximately the same as width.
      (i) Avicularia all distally directed, elongate, pointed ; 24–27 costae, each with 6–8 (often 7) lateral costal fusions ; 5 (sometimes 4) oral spines . . . . 10. ***C. glandulosa*** Lang
      (ii) Avicularia all proximally directed.
        (α) Avicularia with sharply pointed, elongate rostra 11. ***C. aviculosa*** (Lang)
        (β) Avicularia rounded, small or relatively large, occasional, sporadic, never paired ; 14–30 (often about 20) costae ; 4–8 (often 5–7) lateral costal fusions ; 4–5 oral spines 12. ***C. magnifica*** (d'Orbigny)
(D) *Castanopora* with avicularia ; 13–15 costae, each with 6–7 lateral costal fusions ; gymnocyst widely exposed . . . . . . 13. ***C. faujasi*** (Hagenow)
(II) Zoarium cylindro-quadrate, erect ; zooecia of the four adjacent rows alternate ; 20–25 costae . . . . 14. ***C. voigti*** sp. nov.

Cellepora perforata Quenstedt and *Repteschareila radiata* d'Orbigny were both referred to *Rhiniopora* by Lang (1922 : 183, 187). But as their systematic position is very uncertain, they have been omitted from the above key. A discussion of the status of these species is on p. 237.

Rhiniopora hispida Lang is also omitted from the above key ; the holotype, the only specimen, is very badly damaged and worn, making generic and specific diagnosis impossible. The species is discussed on p. 237.

Reptescharipora ornata d'Orbigny, referred to *Castanopora* by Lang (1922 : 213), is also omitted from the above key. The holotype is so poorly preserved that it is not possible to place the species with any certainty at all. The species is discussed on p. 238.

1. *Castanopora armata*[1] sp. nov.

(Pl. 16, fig. 1 ; Text-fig. 103)

HOLOTYPE. D.31717, an encrusting zoarial fragment of about ten zooecia. Maastrichtian, zone of *Belemnella lanceolata* (*O. lunata* Chalk). Southern Bluff, Trimingham, Norfolk. T. H. Withers Collection.

DIAGNOSIS. *Castanopora* with orifice as wide as high ; oral spine-bases 4 ; costae 18–22, each with 4–6 (often 5) lateral costal fusions and pelmatidia ; avicularia of three kinds : one form constantly paired on either side of the orifice, distally directed and elongate ; a second form very prominent, proximally directed, sporadic and variable in position ; a third form also proximally directed, but constantly placed just distally to the orifice.

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[1] Lat., *armare*, " to arm ", referring to the numerous avicularia.

Description. *Zoarium* encrusting, unilaminar. *Zooecia* slightly elongate-oval to broadly oval, very closely placed. *Orifice* about as wide as high, evenly rounded distally and laterally and without proximal-lateral constrictions, the proximal margin straight. *Oral spine-bases* 4, in two pairs placed distally and laterally respectively, all of about the same thickness. *Frontal shield* almost flat, its margins descending sharply at the inner ends of the somewhat slot-like *outer intercostal spaces*. *Costae* 18–22, each with 4–6 (usually 5) *lateral costal fusions* and an equivalent number of pelmatidia. *Apertural bar* only slightly raised, triangular, the apex directed proximally with a very slight median ridge. *Gymnocyst* almost concealed by the closeness of the zooecia and the development of the avicularia : no *interzooecial secondary tissue* present.

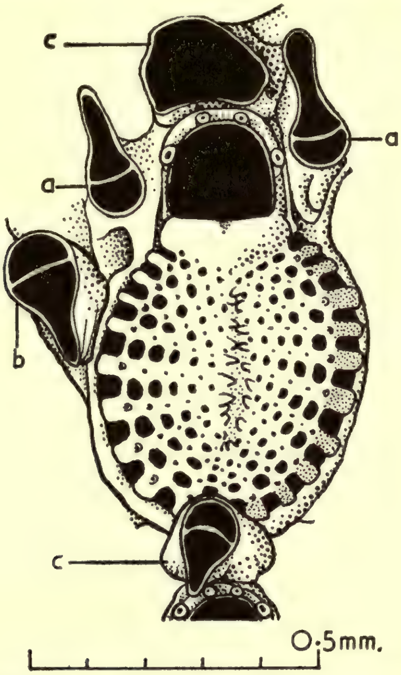


Fig. 103. *Castanopora armata* sp. nov. D.31717. Holotype. Adult zooecium with five avicularia and part of orifice of proximally adjacent zooecium ; *a*, avicularium of form *a* ; *b*, avicularium of form *b* ; *c* avicularium of form *c*.

Avicularia of three kinds : (*a*) a distally directed form, constantly paired one on each side of the orifice, each with a straight or slightly proximally curved *transverse bar*, separating a large, semicircular proximal portion from an elongate, spatulate *rostrum*, the distal end of which is narrower and almost parallel-sided—these avicularia may be directed distally or may tend to embrace the lateral-distal margins of the orifice and point obiquely inwards ; (*b*) proximally directed, sporadic, variable in position, and raised on a very stout stalk with a slightly curved *transverse bar* dividing a lunate or semicircular proximal portion from a pointed *rostrum* with inwardly curving margins ; (*c*) proximally directed, very similar to (*b*) but regularly placed just distally to each orifice. Several broken avicularia of this last type look superficially like broken ovicells. They may be recognized in the broken state by the fact that they do not obscure or interrupt the development of the distal pair of oral spines. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·72 to 0·75 mm.
lz = 0·45 to 0·56 mm.
hr = 0·14 to 0·16 mm.
lr = 0·16 to 0·17 mm.
Avicularia:
Type (*a*) Lz = 0·24 mm.
lz = 0·095 mm.
Type (*b*) Lz = 0·24 mm.
lz = 0·12 mm.
Type (*c*) Not measurable.

REMARKS. D.31717 differs from other species in possessing three types of avicularia. The most unusual type present is the regularly placed, proximally directed avicularium lying immediately distally to each orifice. The occurrence of frequent, proximally directed avicularia, taking into account both types, is unusual at this high stratigraphic level. Lang in fact suggested that the various species of *Castanopora* tend, in successively higher horizons, to have fewer and fewer proximally directed avicularia.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian, zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk).

SPECIMEN. Holotype—see above.

2. ***Castanopora labiata*** (Levinsen)

1907 *Cribrilina labiata* Levinsen, pp. 155, 156, 158, pl. opp. p. 160, figs. 1, 1*a*–*f*.
1916*a* *Rhiniopora labiata* (Levinsen) Lang, p. 96.
1922 *Rhiniopora labiata* (Levinsen) : Lang, p. 186.
1925 *Cribrilina valida* Levinsen, p. 376, pl. 5, figs. 58*a*–*d*—(copy of Levinsen's 1907 figures).
1927 *Cribrilina valida* Levinsen : Voigt, p. 102.
1930 *Cribrilina valida* Levinsen : Voigt, p. 551.

LECTOTYPE. (Chosen by Lang, 1916*a* : 96) Specimen figured by Levinsen, 1907, pl. opp. p. 160, fig. 1. Lower Maastrichtian, zone of *Belemnella lanceolata.* Møen and Aalborg, Denmark.

EMENDED DIAGNOSIS. *Castanopora* with 28–34 costae ; avicularia of two kinds : one form distally directed, very large, vicarious, rare, spatulate, with a straight transverse bar, the other form more frequent, proximally and obliquely directed, small, oval and slightly pointed proximally, with small lateral constrictions.

DESCRIPTION. (Based on Levinsen's description and figure.) *Zoarium* apparently erect, unilaminar. *Zooecia* large, broadly oval. *Orifice* evenly rounded distally and laterally, the sides tending to converge at the straight proximal margin, height of orifice about one-quarter the length of the zooecium. *Oral spines* unknown. *Frontal shield* flat. *Costae* 28–34, each with at least 4 (possibly 5 or 6) *lateral costal fusions*. *Pelmatidia* presumably present, number unknown. *Apertural bar* fairly wide, slightly curved proximally, with a slight median furrow. *Gymnocyst* probably concealed by *interzooecial secondary tissue* with triangular *lacunae*.

Avicularia rare, of two forms : (*a*) distally directed, large, vicarious, sporadic, broadly spatulate, divided by a *transverse bar* into a small, semicircular proximal portion and a very large, distally rounded *rostrum* ; and (*b*) more frequent, proximally directed, unpaired, small [about one half the size of form (*a*)], rounded or slightly pointed proximally, with slight lateral constrictions dividing a semicircular proximal portion from a larger oval-triangular *rostrum*. *Ovicells* not seen.

REMARKS. Levinsen's MSS. and figures were published posthumously in 1925 and edited by Nielsen & Mortensen, who stated (p. 285) that " the first seven plates represent the figures found together with the manuscript ".

On pl. 5, fig. 58*a–d*, appears a copy of Levinsen's 1907 figures of *Cribrilina labiata*. Here (1925), however, the species is called *Cribrilina valida* sp. nov. and it is described as such on p. 376 and 377. It is probable that Levinsen himself, having omitted a description of *Cribrilina labiata* in 1907, regarded the name as invalid, and fully described the form as *Cribrilina valida* intending to re-use the original 1907 figure. But the name *labiata* is valid, and *valida* is a synonym.

Levinsen's description (1925) supersedes that of Lang (1922 : 186) which was based only on Levinsen's 1907 figure. Levinsen described the zoarial habit, but gave no measurements. He stated that there were " no marks of spines "—this may imply that the margins of the orifices were worn obliterating the oral spines.

Lang (1922 : 186) referred the species to *Rhiniopora*. He regarded the marked dimorphism of the avicularia as a primitive feature suggesting affinities with his genus *Castanopora*, which here includes *Rhiniopora*.

The horizon of the species was given by Levinsen (1925) as Senonian, zone of *Belemnitella mucronata*.

STRATIGRAPHICAL DISTRIBUTION. Lower Maastrichtian, zone of *Belemnella lanceolata*.

SPECIMENS. None in the collection.

3. ***Castanopora retrorsa*** Lang

(Pl. 16, fig. 2 ; Text-fig. 104)

1909 *Cribrilina dibleyi* Brydone : White, pp. 34, 39 [*fide* Lang] (*non Cribrilina dibleyi* Brydone, 1906, p. 297, text-fig. 8).

1916*a* *Castanopora retrorsa* Lang, pp. 94, 95.

1922 *Castanopora retrorsa* Lang : Lang, p. 206, pl. 4, fig. 9 ; text-fig. 65.

HOLOTYPE. D.21170. Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *Marsupites*, subzone of *Uintacrinus*, *Uintacrinus* Band. North-west of Newland's Barn, Odiham, Hampshire. L. Treacher Collection.

EMENDED DIAGNOSIS. *Castanopora* with orifice wider than high ; oral spine-bases at least 4 ; costae 21–23, each with 4 (occasionally 3) lateral costal fusions and pelmatidia; avicularia of two kinds: a distally directed, frequently paired form, very long and sharply pointed, and a proximally directed, shorter, pointed form.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Zooecia* relatively large, closely placed, elongate oval. *Orifice* wider than high, evenly rounded distally and laterally, the sides tending to diverge at the straight proximal margin. *Oral spine-bases* at least 4. *Frontal shield* evenly and well arched, possibly flattening slightly in the median area of fusion. *Costae* 21–23, fairly coarse, each with 4 (occasionally 3) *lateral costal fusions* and an equivalent number of *pelmatidia*. The *outer intercostal spaces* are long and slot-like. *Apertural bar* with a small, but distinct, median vertical projection formed by the slightly upturned distal ends of its component costae. *Gymnocyst* concealed by the closeness of the zooecia and the development of avicularia and ovicells.

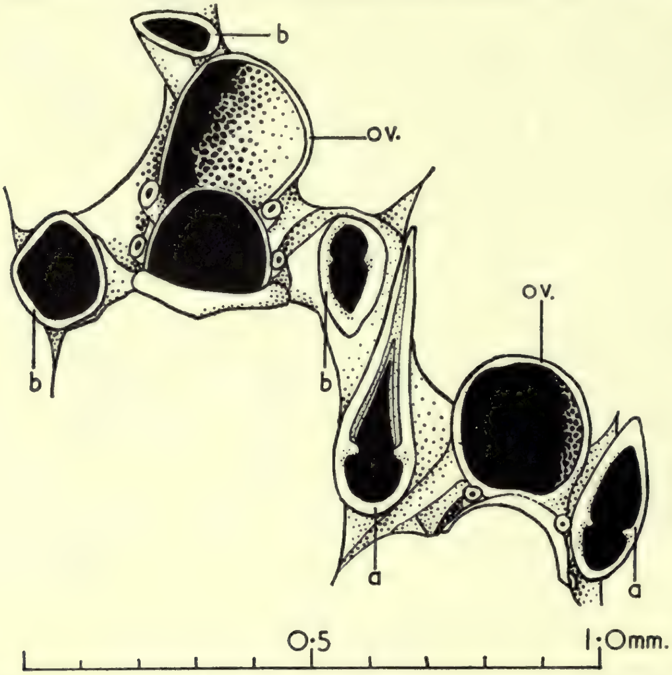


FIG. 104. *Castanopora retrorsa* Lang, D.21170. Holotype. Parts of two adult zooecia (frontal shields not shown) five avicularia and two broken and worn ovicells (*ov.*). *a*, avicularia of form *a*; *b*, avicularia of form *b*.

Avicularia of two kinds: either (*a*) distally directed, usually paired one on each side of the orifice or sometimes unpaired near the orifice, divided by a *transverse bar*, which is distally concave, into a narrow, elongate, acute *rostrum* and a short, somewhat rounded, proximal portion; or (*b*) shorter, proximally directed, usually paired, one on each side of the orifice, or sometimes unpaired near the orifice, divided by a straight *transverse bar* into a somewhat triangular, pointed *rostrum* and a semicircular proximal portion: these avicularia may sometimes be directed proximally outwards. *Ovicells* hyperstomial, large, prominent, high, globular or slightly narrowed, smooth, resting on the frontal shield of the distally adjacent zooecium. The distal pair of oral spines may flank the opening of the ovicell.

MEASUREMENTS. *Zooecia* Lz = 0·84 to 1·06 mm.
lz = 0·50 to 0·59 mm.
hr = 0·15 to 0·18 mm.
lr = 0·18 to 0·21 mm.
Avicularia :
Type (*a*) Lz = 0·39 to 0·42 mm.
lz = 0·12 mm.
Type (*b*) Lz = 0·21 mm.
lz = 0·09 mm.

REMARKS. Lang (1922 : 208) regarded *C. retrorsa* as the most primitive species of *Castanopora.* Stratigraphically it is the earliest, well separated from the main group in the upper part of the zone of *B. mucronata* and in the *O. lunata* Chalk.

The very narrow, distally directed avicularia are particularly distinctive, as are the frequent proximally directed forms. Lang (1922, text-fig. 65) indicated four avicularia—a distally directed pair near the orifice, and a proximally directed pair near the proximal end of the zooecium, which are shown arising from the proximal-lateral areas of the gymnocyst. I have not seen in D.21170 any zooecium which has four definitely associated avicularia : there is either a distally directed pair near the orifice or these are replaced by a proximally directed pair, or one or other of the avicularian forms may occur singly near the orifice.

The widespread development of ovicells in D.21170 tends to obscure the oral spine-bases, which are, however, probably always 4 in number.

Lang regarded *C. retrorsa* as a form radical to the other species of *Castanopora.* Certainly the frequent apparent " replacement " of one form of avicularia by another seems to be a more primitive character. Some of the later species may possess proximally directed avicularia, but they always possess distally directed avicularia of fairly constant shape and position.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *Marsupites,* subzone of *Uintacrinus, Uintacrinus* Band.

SPECIMEN. Holotype—see above.

4. ***Castanopora castanea*** Lang

(Pl. 16, figs. 3–5 ; Text-fig. 105)

1916*a* *Castanopora castanea* Lang, p. 95.
1916*a* *Castanopora nucifera* Lang, p. 95.
1916*a* *Castanopora juglans* Lang, p. 95.
1922 *Castanopora nucifera* Lang : Lang, p. 214, pl. 4, fig. 11 ; text-fig. 67.
1922 *Castanopora juglans* Lang : Lang, p. 215, pl. 5, fig. 1 ; text-fig. 68.
1922 *Castanopora castanea* Lang : Lang, p. 217, pl. 5, fig. 2 ; text-fig. 69.
1923 *Castanopora castanea* Lang : Waters, pp. 548, 558, 560.
1923 *Castanopora juglans* Lang : Waters, pp. 558, 560.
1929 *Castanopora castanea* Lang : Lang, p. 438, text-fig. 39 (24).

1930 *Castanopora castanea* Lang : Voigt, pp. 513, 561, pl. 30, fig. 17.
1935 *Castanopora castanea* Lang : Bassler, p. 65.
1953 *Castanopora castanea* Lang : Bassler, p. G192, text-fig. 144, 21.

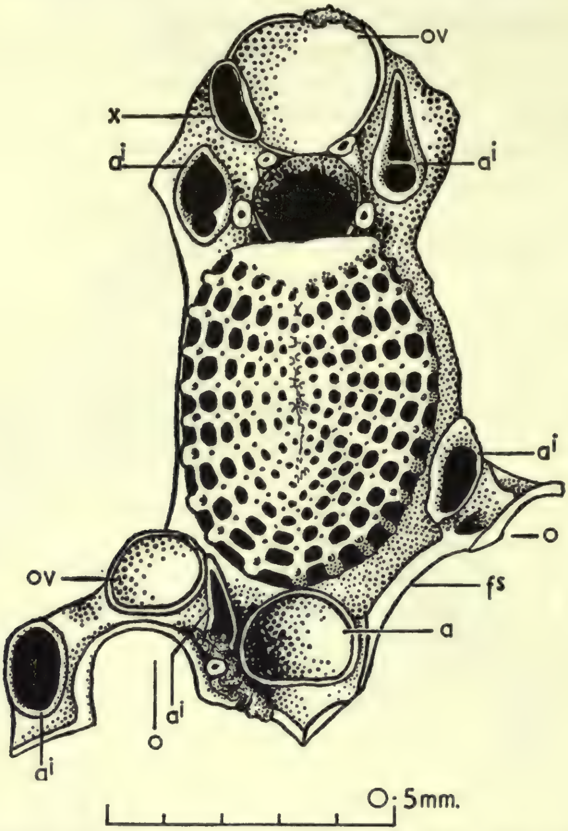


Fig. 105. *Castanopora castanea* Lang, D.16654. Holotype. Adult ovicelled zooecia, showing five distally directed, generally worn avicularia (*a′*) and one sporadic, large, rounded avicularium (*a*). *fs*, broken edge of frontal shield of adjacent zooecium ; *o*, worn orifices of adjacent zooecia ; *ov*, broken and worn ovicells ; *x*, break in the surface—not an avicularium.

Holotype. D.16654. Zoarial fragment encrusting a piece of echinoid test. Horizon given as Senonian, zone of *B. mucronata*—probably boreal Maastrichtian. Rügen. Agnes Laur Collection.

Emended diagnosis. *Castanopora* with orifice wider than high ; 4 oral spine-bases ; 16–23 costae, each with 4–8 (often 6–7) lateral costal fusions and pelmatidia ; avicularia of two kinds—a common, frequently paired, distally directed and pointed form with elongate, triangular rostrum, and an occasional, sporadic form which is large, rounded and probably proximally directed.

Description. *Zoarium* encrusting, unilaminar. *Adult zooecia* closely placed, relatively large, broadly-oval to somewhat elongate-oval. *Orifice* generally somewhat wider than high, not very large, evenly rounded distally and laterally and without proximal-lateral constrictions, the proximal margin straight, usually shorter than the greatest width of the orifice. *Oral spine-bases* 4, of medium size, the lateral pair only slightly thicker than the distal pair. *Frontal shield* very flatly arched or slightly but evenly arched, its margin descending sharply at the inner ends of the *outermost intercostal* spaces which are more slot-like than rounded. *Costae* 16–23, each with 4–8 (often 6–7) *lateral costal fusions* and an equivalent number of *pelmatidia*. *Apertural bar* of variable shape ; either of medium thickness, straight and not very prominent, or fairly wide, triangular, thickened, and slightly expanded proximally in the mid-line : a very slight median ridge may be present, or the median part of the apertural bar may distinctly protrude. None of the apertural bars appears to be furrowed in the mid-line. *Gymnocyst* almost totally concealed due to the closeness of the zooecia and the development of the avicularia : no *interzooecial secondary tissue* present.

Avicularia of two kinds : (*a*) distally directed, elongate, with a long, triangular, pointed *rostrum*, divided by a straight or slightly proximally curved *transverse bar* from the small, semicircular proximal portion. This type is most frequently developed, commonly paired, one on either side of each orifice and placed near the distal-lateral margins, or more occasionally occurring singly on one side or the other of the orifice. (*b*) A second type occurs very occasionally : it is proximally directed, large, rounded, sporadic, and found more commonly in the earlier stages of zoarial growth.

Ovicells hyperstomial, smooth, globular, of medium size but prominent. The opening of the ovicell may be flanked by the distal pair of oral spines.

Young zooecia possess 4 oral spine-bases, the frontal shield is more evenly and markedly arched than that of the adult zooecia but still possesses a relatively flat median area of fusion. Costae 14 or 15, each with ?4 lateral costal fusions and ?an equivalent number of pelmatidia. Apertural bar much less prominent than in the adult zooecia. Definitely paired, distally directed avicularia are scarce. One large, rounded, proximally directed avicularium of the second type described above occurs between two zooecia of the second ring round the ancestrula in specimen N.C.M.76–937 (27/1).

MEASUREMENTS. *Adult zooecia* Lz = 0·78 to 1·00 mm.
lz = 0·50 to 0·75 mm.
hr = 0·12 to 0·15 mm.
lr = 0·15 to 0·18 mm.
Avicularia :
Type (*a*) Lz = 0·27 to 0·39 mm.
lz = 0·12 mm.
Type (*b*) Lz = 0·21 mm.
lz = 0·18 mm.
Young zooecium Lz = 0·57 mm.
lz = 0·39 mm.
hr = 0·15 mm.
hr = 0·15 mm.

REMARKS. *Castanopora juglans* Lang and *C. nucifera* Lang are here regarded as synonymous with *C. castanea* Lang.

All the available specimens previously assigned to *C. castanea*, *C. juglans* and *C. nucifera* have been re-examined. Three specimens had been assigned to *C. castanea*, and *C. nucifera* was represented only by the holotype (D.15600). Though the latter has a more delicate structure than the specimens of *C. castanea* and has a slightly arched frontal shield, these differences are probably due to somewhat different growth conditions. But in both species the size and shape of the zooecia are closely similar ; there are 4 oral spine-bases ; the orifice tends to be wider than high ; there are 16–23 costae, and often 6 or 7 lateral costal fusions on each costa (in D.15600 there may be 8 lateral costal fusions present between some costae) ; the distally directed avicularia are similar in position and type ; and both species also have very occasional, rounded, sporadic, proximally directed avicularia. The horizon of both species is Senonian, zone of *B. mucronata*.

C. juglans is represented in the collection by the holotype (D.15608) and one other specimen (D.30110). According to Lang (1922 : 216) " *C. juglans* differs from *C. nucifera* . . . only in the shape of the aperture [orifice] and in the width of the apertural bar. It is of interest as being, in both respects, a connecting link between *C. nucifera* and *C. castanea* ".

The shape of the orifice of the specimens assigned to *C. juglans* differs from that of *C. castanea* only very slightly and the same relationship between height and width is maintained. Beyond using the values of hr and lr, which appear to be relatively constant for a given species, it is very difficult to apply a fine division of shapes of orifices as a diagnostic feature. In *C. castanea*, *C. juglans* and *C. nucifera*, hr is almost always less than lr but the shape of the orifice may vary slightly even within a single zoarium. I do not regard slight widening or thickening of the apertural bar as of diagnostic value. A marked median ridge or process is a definite feature which can be used, in conjunction with other zooecial characters, for specific diagnosis, but slight variations in the width or thickness of the apertural bar occur frequently in different zooecia of the same zoarium. In the material examined and here assigned to *C. castanea*, such variations within single zoarial fragments were frequently found. Lang himself regarded *C. juglans* as a linkage form between *C. castanea* and *C. nucifera* : the three belong to a single species. The holotype of *C. castanea* is well preserved : in one part two zooecia coalesce and share a single orifice.

Voigt (1930 : 513, pl. 30, fig. 17) briefly noted and figured a specimen which he assigned to *C. castanea* Lang. The horizon is again Upper *B. mucronata* Zone of Rügen. The measurements given and the range in number of costae agree with the material which has here been revised.

Specimens N.C.M.76.937(27/1–4) are parts of a previously undescribed zoarium also placed in *C. castanea* ; much of the early growth stages of the zoarium is fairly well preserved and the description and measurements of the young zooecia of the species are based on parts of this zoarium.

STRATIGRAPHICAL DISTRIBUTION. Senonian, upper part of zone of *B. mucronata*, and Maastrichtian, zone of *Belemnella lanceloata* (*O. lunata* Chalk), and boreal Maastrichtian of Rügen.

SPECIMENS. D.16654. Holotype—see above.

D.14990. Zoarial fragment encrusting a piece of echinoid test. Specimen badly damaged and worn, labelled " *C. castanea* Lang ", but the identification is here questioned. Horizon given as Senonian, zone of *B. mucronata*, Rügen, but probably boreal Maastrichtian. Agnes Laur Collection.

D.15347. Zoarial fragment encrusting a piece of echinoid test. Labelled " Senonian, zone of *B. mucronata*, Rügen ", probably Maastrichtian. Agnes Laur Collecton.

D.15600. Zoarial fragment encrusting a piece of echinoid test. Holotype of *C. nucifera* Lang. Maastrichtian, zone of *Belemnella lanceolata* (*O. lunata* Chalk). Trimingham, Norfolk. A. C. Savin Collection.

D.15608. Zoarial fragment encrusting a piece of echinoid test. Holotype of *C. juglans* Lang. Horizon, locality and collection as for D.15600.

D.30110. Zoarial fragment labelled " *C. juglans* Lang " encrusting a fragment of an *Ostrea lunata*. Horizon, locality and collection as for D.15600.

OTHER MATERIAL. N.C.M.76.937(27/1–4). Parts of an extensive zoarium with young zooecia, encrusting four fragments of the same echinoid test. Senonian, zone of *B. mucronata*. Weybourne Mill, Weybourne, Norfolk. R. M. Brydone Collection.

5. *Castanopora dibleyi* (Brydone)

(Pl. 16, figs. 6–8 ; Pl. 17, figs. 1, 2 ; Text-figs. 106, 107)

1906 *Cribrilina dibleyi* Brydone, p. 297, text-fig. 8.
1909 *non Cribrilina dibleyi* Brydone : White, pp. 34, 39.
1913 *Cribrilina dibleyi* Brydone : Brydone, p. 437, pl. 14, fig. 9.
1916*a* *Castanopora dibleyi* (Brydone) Lang, pp. 94, 95.
1921 *Castanopora dibleyi* (Brydone) : Lang, p. xci.
1922 *Castanopora dibleyi* (Brydone) : Lang, p. 209, pl. 14, fig. 10 ; text-fig. 66*a*, *b*.
1923 *Castanopora dibleyi* (Brydone) : Waters, pp. 548, 559, 560.
1929 *Castanopora dibleyi* (Brydone) : Lang, p. 438, text-figs. 39 (22, 23).
1930 *Castanopora dibleyi* (Brydone) : Voigt, pp. 512, 543, 561, pl. 30, fig. 18.
?1930 *Castanopora* sp. Voigt, pp. 512, 561, pl. 30, fig. 20.

LECTOTYPE. (Chosen by Lang, 1922 : 210.) S.M., B.36115. A very large fragment of zoarium, with some young zooecia, encrusting a piece of echinoid test. Two zooecia of this specimen were figured by Brydone (1906 : 297, text-fig. 8) as *Cribrilina dibleyi*, and chosen by Lang as lectotype of *Castanopora dibleyi*. Maastrichtian, zone of *Belemnella lanceolata* (*O. lunata* Chalk). Trimingham, Norfolk. R. M. Brydone Collection.

EMENDED DIAGNOSIS. *Castanopora* with orifice as wide as, or slightly wider than, high ; oral spine-bases usually 4 (occasionally 5) ; costae 16–20, each with 5, 6 or 7 lateral costal fusions and pelmatidia ; avicularia of two kinds : a constantly paired, distally directed, elongate, pointed form near the orifice, and a proximally directed, less frequent, sporadic, pointed form.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Adult zooecia* relatively small, broadly oval, some almost circular in outline ; very closely placed. *Orifice* slightly wider than high or of equal height and width, straight sided but rounded distally, straight posteriorly; there are no proximal-lateral constrictions. *Oral spine-bases* commonly 4, the lateral pair usually thicker than the distal pair, a fifth small, slender, median, distal oral spine may be present. *Frontal shield* broad, often almost circular in outline, very flatly arched, not sharply descending at the margin. *Costae* 16–20, each with 5, 6 or 7 *lateral costal fusions* and an equivalent number of *pelmatidia*, each of which may be surrounded by a small rim producing a minute boss-like process opposite each lateral costal fusion: this is well seen in the lectotype. *Apertural bar* not prominent, somewhat swollen at either end; a very slight median ridge may be present. *Gymnocyst* only very occasionally exposed where the closeness of the zooecia and the development of avicularia have not obscured it.

Avicularia of two kinds: (*a*) a constantly paired form placed one on either side of and close to the orifice, distally directed, elongate and pointed, divided by a slightly curved *transverse bar* into a semicircular proximal portion and a very elongate, narrow, triangular or spatulate *rostrum*; (*b*) a proximally directed, infrequent, sporadic form, similar to type (*a*) but probably slightly shorter.

Ovicells hyperstomial, prominent, smooth, globular, slightly laterally compressed near the front, often with a broad median ridge. The lateral pair of oral spines may flank the entrance to the ovicell.

Young zooecia smaller and relatively less broad than the adult zooecia. Orifices as wide as, or slightly wider than, high. Oral spine-bases 4 or 5, the latter number apparently occurring more frequently in the younger zooecia. Frontal shield more roundly arched than in the adult. Costae 11–15, each with 4 or 5 lateral costal fusions. The apertural bar of the ancestrula of D.8003 has a slight median, proximal bend, but the zooecia in the first ring have straight apertural bars. Gymnocyst not visible in the circum-ancestrular area. Avicularia not paired on the ancestrula. The typically paired form which is distally directed on either side of the orifice occurs in the first ring of zooecia. The rostra of these avicularia tend to be directed outwards (in the adult the paired avicularia near the orifice are more parallel to its mid-line). Between two zooecia of the first ring round the ancestrula of D.8003 is a proximally directed, slightly pointed, avicularium, which is larger than the avicularia of type (*a*) in the same ring of zooecia. Proximally directed avicularia possibly occur more frequently in the circum-ancestrular area than in the adult parts of the zoarium, but, as in S.M., B.36267, they may be quite abundant locally in ovicelled parts of the adult zoarium.

MEASUREMENTS. *Adult zooecia* Lz = 0·66 to 1·00 mm.
lz = 0·54 to 0·67 mm.
hr = 0·12 to 0·19 mm.
lr = 0·12 to 0·19 mm.
Young zooecia
(of S.M., B.36267) Lz = 0·50 to 0·55 mm.
lz = 0·32 to 0·40 mm.
hr = 0·10 to 0·11 mm.
lr = 0·12 to 0·13 mm.

Ancestrula
(of D.8003) Lz = 0·42 mm.
lz = 0·24 mm.
hr = 0·095 mm.
lr = 0·090 mm.

Avicularia
(in adult part of zoarium) :
Type (*a*) Lz = 0·21 to 0·43 mm.
lz = 0·065 to 0·14 mm.
Type (*b*) Lz = 0·27 to 0·30 mm.
lz = 0·10 to 0·19 mm.

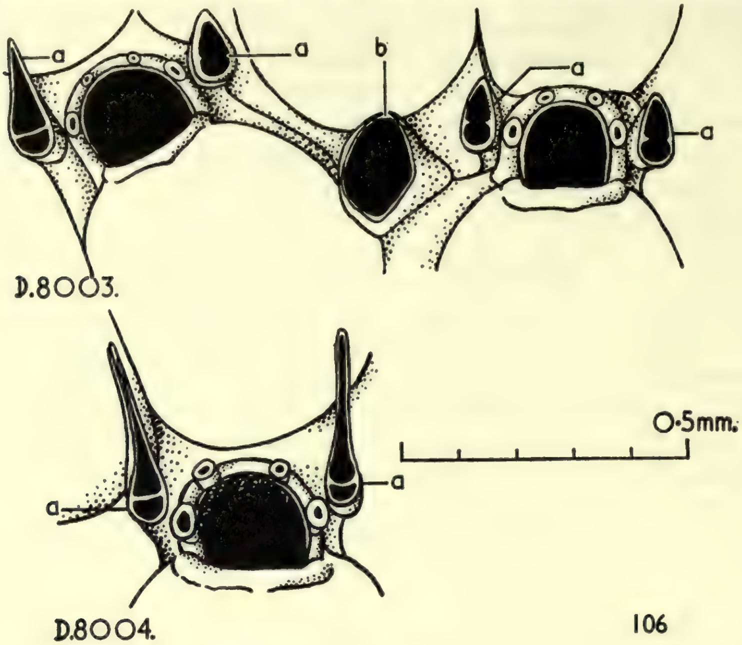
(Associated with the ancestrula of D.8003)
Type (*a*) Lz = 0·085 mm.
lz = 0·050 mm.

(Associated with the first ring of zooecia of D.8003)
Type (*a*) Lz = 0·125 mm.
lz = 0·060 mm.
Type (*b*) Lz = 0·180 mm.
lz = 0·155 mm.

REMARKS. All the available specimens of *C. dibleyi* (Brydone) in the British Museum (Natural History) have been re-examined, as well as those figured by Brydone (1906 : 297, text-fig. 8—the lectotype S.M., B.36115 ; 1913 : 437, pl. 14, fig. 9—S.M., B.36267). D.8003 and S.M., B.36267 are of particular interest : the former is labelled as a metatype and has a well-preserved ancestrula and circum-ancestrular area ; the latter also possesses young zooecia close to the ancestrula. The description of the young zooecia is based largely on these specimens. In D.8004 well-preserved proximally directed avicularia are present in addition to some very young zooecia. D.15599 also has a preserved ancestrula and numerous broken ovicells. D.20609 is a very worn zoarial fragment encrusting a piece of *Inoceramus* shell—fairly young zooecia are present, but the preservation is poor and the identification as *Castanopora dibleyi* is here queried. All the specimens are from the Maastrichtian, zone of *Belemnella lanceolata* (*O. lunata* Chalk) of Trimingham, Norfolk, except for D.20609 which is from the Senonian, zone of *B. mucronata*, also from Norfolk. Apart from *C. retrorsa* apparently no other species of *Castanopora* occur below the zone of *B. mucronata*.

Voigt (1930 : 512, pl. 30, fig. 18) briefly described a specimen as *C. dibleyi* (Brydone). The measurements and the number of costae agree with those given above. The reference to " comparatively short and blunt " avicularia apparently refers to worn examples. The figure shows no elongate pointed avicularia, those shown all appearing to be somewhat worn. It is probable that the specimen referred to *Castanopora* sp. by Voigt (1930 : 512, 561, pl. 30, fig. 20) is also *C. dibleyi* (Brydone).

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian, zone of *Belemnella lanceolata* (*O. lunata* Chalk) and Senonian, zone of *B. mucronata* in England, and boreal Maastrichtian of Rügen.



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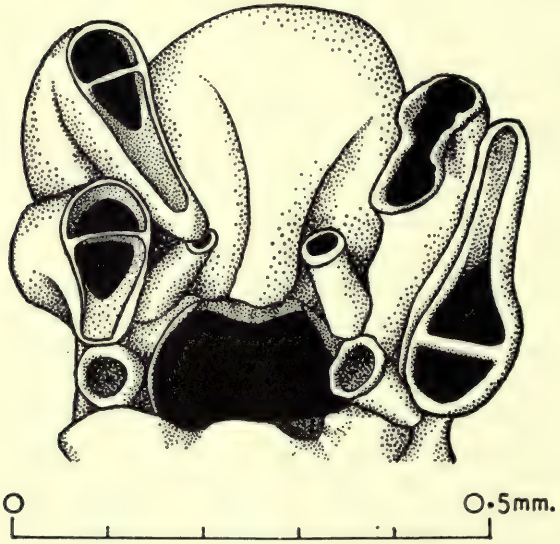

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FIGS. 106–107. *Castanopora dibleyi* (Brydone).

(106) D.8003—metatype and D.8004. Orifices and avicularia of three adult zooecia (frontal shields not shown). Avicularia of two kinds: *a*, paired, distally pointed and directed; *b*, occasional, sporadic, interzooecial.

(107) S.M., B. 36267. Figured Brydone (1913, pl. 14, fig. 9) as *Cribrilina dibleyi*. Orifice of adult ovicelled zooecium with four avicularia. Proximally directed avicularia of type *b* occur more frequently than is usual in other specimens of *Castanopora dibleyi* examined here. Possibly type *b* avicularia develop particularly in association with ovicelled zooecia, especially where development of the ovicell has apparently disturbed the normal development of the distally directed avicularia of type *a*.

SPECIMENS. D.8003. Zoarial fragment with ancestrula, encrusting a piece of echinoid test. Labelled " metatype specimen ". Horizon, locality and collection as for the lectotype.

D.8004. Zoarial fragment encrusting a piece of echinoid test. Horizon, locality and collection as for the lectotype.

D.15599. Zoarial fragment encrusting a piece of echinoid test. Horizon and locality as for the lectotype. A. C. Savin Collection.

D.20609. Part of a worn zoarium encrusting a fragment of *Inoceramus* shell. Labelled by Lang " *C. dibleyi* (Brydone) ", but the determination is doubtful. Senonian, zone of *B. mucronata.* Norwich, Norfolk. T. G. Bayfield Collection.

OTHER MATERIAL. S.M., B.36115. Lectotype—see above.

S.M., B.36267. Zoarial fragment with ovicelled and very young zooecia encrusting a piece of echinoid test. [Part of this specimen was figured by Brydone (1913 : 437, pl. 14, fig. 9) as *Cribrilina dibleyi*]. Horizon, locality and collection as for the lectotype.

6. ***Castanopora guascoi*** (Ubaghs)

1865 *Escharipora guascoi* Ubaghs, p. 51, pl. 2, fig. 3*a–c*.
1913 *Cribrilina guascoi* (Ubaghs) Brydone, p. 437.
1916*a* *Castanopora guascoi* (Ubaghs) Lang, pp. 95, 96.
1922 *Castanopora guascoi* (Ubaghs) : Lang, p. 221.
1930 *Castanopora guascoi* (Ubaghs) : Voigt, pp. 512, 561, pl. 31, fig. 1.

LECTOTYPE. (Chosen by Lang, 1922 : 221.) The specimen figured by Ubaghs, 1865, pl. 2, fig. 3*b*. Maastrichtian, Valkenburg (Fauquemont), east of Maastricht, Limbourg, Holland.

EMENDED DIAGNOSIS. *Castanopora* with orifice wider than high ; oral spine-bases probably 5 or 6 ; costae 18–20 ; gymnocyst well exposed ; avicularia of two kinds, a distal-lateral pair, apparently proximally directed, near each orifice, and an occasional, unpaired, sporadic, proximally directed form.

DESCRIPTION. (Based on Ubaghs' and Voigt's figures.) *Zoarium* encrusting or erect, uni- or bilaminar. *Zooecia* relatively broad, elliptical. *Orifice* wider than high, evenly rounded distally and laterally, the sides tending to converge at the straight proximal border. *Oral spine-bases* fairly large, of uncertain number, definitely more than 4, probably 5 or 6. *Frontal shield* flat, descending sharply at the outer ends of the costae. *Costae* 18–20. Number of *lateral costal fusions* and *pelmatidia* unknown, but probably few. *Apertural bar* fairly prominent, swollen at each end, somewhat rounded, not very thick, straight, with no marked median-proximal widening. *Gymnocyst* well exposed, much more so than in other species of *Castanopora*, visible laterally and proximally to each frontal shield ; no *inter-zooecial secondary tissue.*

Avicularia of two kinds : (*a*) a distal-lateral pair near each orifice, each with a straight *transverse bar*, orientation uncertain, possibly proximally directed ; (*b*) an occasional, sporadic form, proximally directed, elongate and pointed, divided by a straight *transverse bar* into a small semicircular proximal portion and an elongate, triangular *rostrum*. *Ovicells* not seen.

MEASUREMENTS. (According to Voigt, 1930 : 512.)

Zooecia Lz = About 1·0 mm.
lz = 0·60 mm.

REMARKS. The emended diagnosis and description of *C. guascoi* are based on a consideration of Ubaghs' original description and figure and Voigt's description and figure of a specimen from Maastricht.

Voigt (1930 : 512) mentioned the zoarial habit, size of zooecia, and number of costae, and his figure (pl. 31, fig. 1) also shows sporadic avicularia and more than four oral spine-bases. The nature of the paired avicularia is not determinable from the photograph.

Ubaghs (1865 : 51) in his original description referred to a " distal bulge hiding the ovicell ", suggesting that the ovicell, as with other species of *Castanopora*, is hyperstomial. He also mentioned that " above the orifice, almost at the foot of the following cell [zooecium] there is found, on either side of the aforementioned orifice, a depression in which there lies an angular, non-marginate, lateral pore " [translation]. This could refer to worn, paired avicularia, and similar worn avicularia appear to be present in the specimen figured by Voigt.

Ubaghs compared his original specimen with *Escharipora pretiosa* d'Orbigny [=*E. magnifica* d'Orbigny] which Lang (1922 : 212) also referred to *Castanopora*. Ubaghs stated that *E. guascoi* " has several similarities with *E. pretiosa* d'Orbigny, but may be distinguished from it by the lateral pores, which in d'Orbigny's species are elongate, slit-like and marginate. Also the cells [zooecia] of d'Orbigny's species are more elongate and show more rows of pores [intercostal spaces] piercing the cell surface [frontal shield] ... Apart from this, our species (*E. guascoi*) shows, between the rows of cells, " blister-like ", elongate slits, which are rounded above [distally] and " turned down " below [proximally]. I am of the opinion that these should be regarded as avicularia ... " [translation]. In his figure of *E. guascoi* Ubaghs showed this second type of proximally directed sporadic avicularium ; a similar avicularium is shown in the photograph of Voigt's specimen from Maastricht.

Until more specimens are available the description of *Castanopora guascoi* must rest on the interpretation of Ubaghs' and Voigt's figures. One of the most important features—the nature of the paired avicularia near the orifice—is still not determinable ; apart from this most of the other diagnostic characters are reasonably clear and the described specimens are retained as a separate species of *Castanopora*.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian.

SPECIMENS. None in the collection.

7. ***Castanopora spooneri*** (Butler & Cheetham)

1958 *Rhiniopora spooneri* Butler & Cheetham, p. 1154, text-figs. 1, 2.

HOLOTYPE. Louisiana State University Geology Museum 1390. " ... from a chalk bed exposed at Rayburn's dome, Bienville Parish, Louisiana ... equivalent to the Upper Cretaceous Saratoga Chalk of Arkansas ... ".

PARATYPE. L.S.U. Geology Museum 1391. Horizon and locality as for the holotype.

EMENDED DIAGNOSIS [Based on Butler & Cheetham's diagnosis and detailed description and figures (1958 : 1154–1156).] *Castanopora* with small zooecia ; orifice of equal height and width or wider than high ; oral spine-bases 5 ; frontal shield with 14–20, usually 16–18 costae, each with 4–6 inconspicuous pelmatidia with 4 or 5 lateral costal fusions ; apertural bar curved, with a small median process ; gymnocyst concealed by the closely spaced zooecia ; avicularia interzooecial, of one kind only, distally pointed and directed without transverse bars or condyles ; ovicells hyperstomial, prominent, large, globular or somewhat elongate with a median, longitudinal ridge.

MEASUREMENTS. (According to Butler & Cheetham, 1958 : 1156.)

Zooecia Lz = 0·26 to 0·34 mm.
lz = 0·17 to 0·27 mm.
hr = 0·04 to 0·07 mm.
lr = 0·06 to 0·09 mm.
Avicularia Lz = 0·11 to 0·15 mm.
lz = 0·11 to 0·15 mm.

REMARKS. The holotype and paratype specimens of *Rhiniopora* [=*Castanopora*] *spooneri* encrust the inner surfaces of valves of *Ostrea vesicularis* and *Inoceramus*.

The most distinctive features of the species are the small dimensions of the adult zooecia and the character and size of the avicularia. These features, combined with the range in number of the costae, pelmatidia and lateral costal fusions, clearly distinguish the species.

STRATIGRAPHICAL DISTRIBUTION. Upper Cretaceous, equivalent of the Saratoga Chalk of Arkansas, U.S.A. The Saratoga Chalk was placed in the lower part of the Maastrichtian by Stephenson *et. al.* (1942, Chart 9, opp. p. 448).

SPECIMENS. None in the collection.

8. ***Castanopora multicostata*** Voigt

1930 *Castanopora multicostata* Voigt, pp. 512, 561, pl. 30, fig. 19.

LECTOTYPE. Specimen figured by Voigt, 1930, pl. 30, fig. 19. Horizon given as " Senonian, upper part of zone of *B. mucronata*. Rügen "—probably boreal Maastrichtian.

DIAGNOSIS. *Castanopora* with orifice generally wider than high ; oral spines 5–6 ; 26–30 costae, each with about 9 lateral costal fusions ; avicularia of possibly only one type, distally directed, paired near the orifice, pointed, elongate.

DESCRIPTION. Voigt described the species as follows : " *Zoarium* encrusting. *Zooecia* about 0·9 mm. long and 0·55 to 0·60 mm. wide, elliptical. *Gymnocyst* very slightly developed. *Frontal shield* formed of about 30 very closely placed *costae*, between which there are, on average, 9 *lateral costal fusions*. *Orifice* 0·15 mm. high, 0·15 to 0·20 mm. wide, with 5–6 *oral spines* (=' normal ' orifice of Lang).

" *Avicularia* mainly paired, beside orifice, between 0·25 and 0·45 mm. long, distally directed, elongate, pointed " [translation].

To these characters it is possible to add the following from Voigt's figure : *Zoarium* unilaminar. *Zooecia* not so closely placed as in other species of *Castanopora*. *Orifice* generally wider than high, relatively small, evenly rounded distally and laterally, proximal margin straight. The lateral pair of *oral spine-bases* tend to be larger than the others. *Frontal shield* flatly arched ; *costae* 26–30. *Apertural bar* fairly thick and prominent, slightly swollen at each end, bluntly triangular, with the apex proximally directed. *Gymnocyst* exposed laterally and proximally to each frontal shield.

Avicularia apparently of one type only, divided by a straight *transverse bar* into a small semicircular proximal portion and a narrowly elongate, acute, triangular *rostrum* ; placed near the distal-lateral margins of the orifice. *Ovicells* not described or figured.

MEASUREMENTS (*vide* Voigt).

Zooecia Lz = About 0·90 mm.
lz = 0·55 to 0·60 mm.
hr = 0·15 mm.
lr = 0·15 to 0·20 mm.
Avicularia Lz = 0·25 to 0·45 mm.
lz not given.

REMARKS. In his observations on *C. multicostata* Voigt stated (1930 : 513), " The figure (pl. 30, fig. 19) is interesting in that two ' lobes ' of the same colony coalesce and that in the critical zone (where the two growing branches of the zoarium meet) the zooecia appear to be deformed in several ways. In parts, several zooecia have coalesced and others have been constricted and have not developed an orifice, so that they appear as ' rosettes '. This situation is, of course, only possible because of the intercommunication of the individuals. From several *Castanopora* species from the Rügen chalk, described by Lang, this species is distinguished by its large number of costae, and, at the same time, the small size of the zooecia. The nearest species appears to be *Castanopora magnifica* (d'Orb.) which is 1·14 to 1·26 mm. long and which possesses 12 oral spines—as far as can be seen from d'Orbigny's drawing. Apart from this, the French species is bilamellar " [translation].

The large number of costae and lateral costal fusions and the occurrence of 5 or 6 oral spines are distinctive features of *C. multicostata* Voigt. The generally small size of the zooecia, and of the orifices, may also be diagnostic. Only a relatively small area of zoarium is shown in Voigt's figure, and no sporadic, more rounded and proximally directed avicularia, such as usually occur in other species of *Castanopora* from Rügen, can be seen.

STRATIGRAPHICAL DISTRIBUTION. Given as " Senonian, upper part of zone *B. mucronata* ", but probably boreal Maastrichtian.

SPECIMENS. None in the collection.

9. *Castanopora jurassica* (Gregory)

(Pl. 17, figs. 3–5 ; Text-figs. 108, 109)

1894	*Membranipora jurassica* Gregory, p. 62, text-fig. 1.
1896	*Membranipora jurassica* Gregory : Gregory, p. 212, text-fig. 21.
1897	*Membranipora jurassica* Gregory : Woodward, pp. 63, 64, text-fig. 107.
1907	*Membranipora jurassica* Gregory : Bather, pp. 120, 122, text-fig. 65.
1916*a*	*Rhiniopora jurassica* (Gregory) Lang, p. 96.
1916*a*	*Rhiniopora scabra* Lang, pp. 96, 97.
1922	*Rhiniopora scabra* Lang : Lang, p. 196, pl. 4, fig. 7 ; text-fig. 62.
1922	*Rhiniopora jurassica* (Gregory) : Lang, p. 197.
1930	*Rhiniopora scabra* Lang : Voigt, p. 551.

HOLOTYPE. D.180, large fragment of worn and damaged zoarium partly embedded in matrix. Very probably Maastrichtian. Maastricht. Old Collection.

EMENDED DIAGNOSIS. *Castanopora* with orifice wider than high ; zooecia up to 1·45 mm. long ; oral spine-bases 6 ; costae 25–30, each with 8 lateral costal fusions and pelmatidia ; avicularia sporadic, frequent.

DESCRIPTION. *Zoarium* encrusting, unilaminar. *Zooecia* oval, large. *Orifice* wider than high, evenly rounded distally, with straight sides converging somewhat at the straight proximal margin. *Oral spine-bases* 6, occurring in two groups of three on the distal lateral margins of the orifice or as a distal and two lateral-distal pairs, the most proximal pair largest. *Frontal shield* flat, descending quite sharply at the inner ends of the *outermost intercostal spaces*, which are more often slot-like than rounded. *Costae* 25–30, each with 8 *lateral costal fusions* and *pelmatidia*. *Apertural bar* prominent, not very wide, straight, with a small, median ridge on the frontal shield. *Gymnocyst* exposed proximally, and to a less extent laterally, to the frontal shield : no *interzooecial secondary tissue*.

Avicularia fairly frequent, sporadic, probably proximally directed, unpaired, placed near the distal-lateral margins of the orifice, relatively large, oval or slightly pointed proximally.

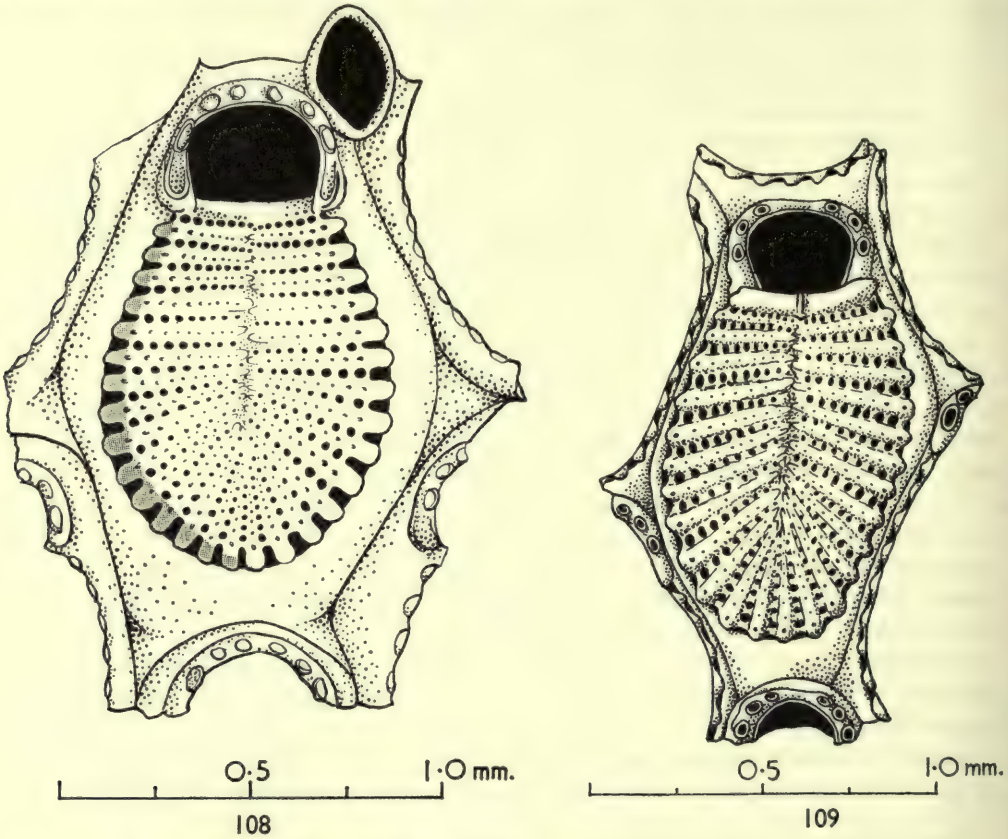
Ovicells probably hyperstomial, apparently globular, prominent, and overlapping on to the distally adjacent zooecium : seen only in the broken state.

MEASUREMENTS. *Zooecia* Lz = 1·18 to 1·45 mm.
lz = 0·66 to 0·81 mm.
hr = 0·21 mm.
lr = 0·24 to 0·33 mm.
Avicularia Lz = 0·27 to 0·36 mm.
lz = 0·21 mm.

REMARKS. Gregory (1894 : 62) incorrectly assigned D.180 to the genus *Membranipora* and to the Jurassic (to the Calcaire à polypiers, Bathonian, of Ranville, Normandy, France). Lang (1916*a* : 96 and 1922 : 197) recognized its cribrimorph structure and its very probable Maastrichtian age and referred it to his genus *Rhiniopora*.

Both *Rhiniopora jurassica* (Gregory) and *R. scabra* Lang are synonymous and belong to *Castanopora*. It is unfortunate that the misleading specific name *jurassica* has to be retained for a Cretaceous species but, as it has priority of publication, no other course is open.

In the holotype (D.14207) of *Rhiniopora scabra* Lang only one complete zooecium is preserved. The dimensions of this and surrounding broken zooecia are the same as those of the two available specimens (D.180 and D.3313) of *Castanopora jurassica* (Gregory), and the number of costae in the complete zooecium of D.14207 is 25, each with 8 lateral costal fusions and pelmatidia, compared with 25–30 costae each with 8 lateral costal fusions and pelmatidia in D.180 and D.3313. The measurements given by Lang for *R. scabra* and *R. jurassica* were overestimated, and, in the latter species, avicularia are fairly frequent rather than "few". Lang stated "the preservation, both of the type specimen [D.180] and of D.3313 is but poor; the detailed characters, therefore, are uncertain". However, careful examination of



FIGS. 108, 109. *Castanopora jurassica* (Gregory).
(108) D.180. Holotype. Adult zooecium and parts of five adjacent, worn zooecia and worn, slightly pointed, probably proximally directed avicularium.
(109) D.14207. Holotype of *Rhiniopora scabra* Lang. Adult zooecium and parts of six adjacent worn zooecia.

the more complete zooecia in these specimens reveals most of the diagnostic characters.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian.

SPECIMENS. D.180. Holotype—see above.

D.3313. Large fragment of worn and damaged zoarium partly embedded in matrix. Maastrichtian. Maastricht, Holland. Old Collection.

D.14207. Holotype of *Rhiniopora scabra* Lang. Worn zoarial fragment. Horizon given as " Senonian, zone of *B. mucronata*, Rügen ", but probably boreal Maastrichtian. Agnes Laur Collection.

10. ***Castanopora glandulosa*** Lang

(Pl. 18, fig. 1 ; Text-fig. 110)

1916*a* *Castanopora glandulosa* Lang, pp. 95, 96.
1922 *Castanopora glandulosa* Lang : Lang, p. 219, pl. 5, fig. 3 ; text-fig. 70,
1923 *Castanopora glandulosa* Lang : Waters, pp. 548, 558, 560.
1930 *Castanopora glandulosa* Lang : Voigt, p. 551.

HOLOTYPE. D.15009, zoarial fragment. Horizon given as " Senonian, zone of *B. mucronata*, Rugen "—probably boreal Maastrichtian. Agnes Laur Collection.

EMENDED DIAGNOSIS. *Castanopora* with very flatly arched frontal shield ; orifice generally of equal height and width ; oral spine-bases 5 (occasionally 4) ; costae 24–27, each with 6–8 (often 7) lateral costal fusions and pelmatidia ; avicularia frequently paired, probably all distally directed, elongate and pointed.

DESCRIPTION. *Zoarium* encrusting or erect, unilaminar. *Zooecia* elongate-oval. *Orifice* generally as wide as high, relatively large, evenly rounded distally and laterally and without proximal-lateral constrictions, the proximal margin straight. *Oral spine-bases* 5 (occasionally 4), all relatively small, but the lateral pair tend to be larger, a fifth distal median oral spine is sometimes present. *Frontal shield* evenly, but flatly, arched. *Costae* 24–27, each with 6–8 (often 7) *lateral costal fusions* and an equivalent number of *pelmatidia*. *Apertural bar* flat, relatively wide with a slight thickening at the ends, triangular, the apex pointing proximally ; no median ridge or furrow. *Gymnocyst* only slightly exposed, mainly proximally to the frontal shield, but largely concealed owing to the closeness of the zooecia : no interzooecial secondary tissue present.

Avicularia of one kind : frequently, but not always, paired, one on each side of the orifice near the distal-lateral margins. There are apparently no proximally directed avicularia. In the one specimen available, all the avicularia are broken, but they were very probably of the same type as in *C. castanea*. It is possible to see the broken proximal ends of some avicularia ; one of these possesses constrictions marking the position of a broken *transverse bar*. All the evidence suggests that all the avicularia are distally directed. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·93 to 1·12 mm.
lz = 0·50 to 0·64 mm.
hr = 0·18 mm.
lr = 0·18 mm.
Avicularia Not measurable.

REMARKS. Only the holotype, a zoarial fragment, is available. In his diagnosis of this species Lang (1922 : 219) suggested that occasionally proximally directed avicularia may be present : I cannot see any indications of these. The zooecial length was slightly overestimated as 1·25 to 1·50 mm., although the generally larger size of this species is still apparent from the measurements given above. The range in number of costae (24–27) is generally above that of other species. The zoarium may have been encrusting. Lang stated that the number of oral spines is 4, and in the ensuing description he referred to 5 : both numbers occur as described, but the latter arrangement is more frequent.

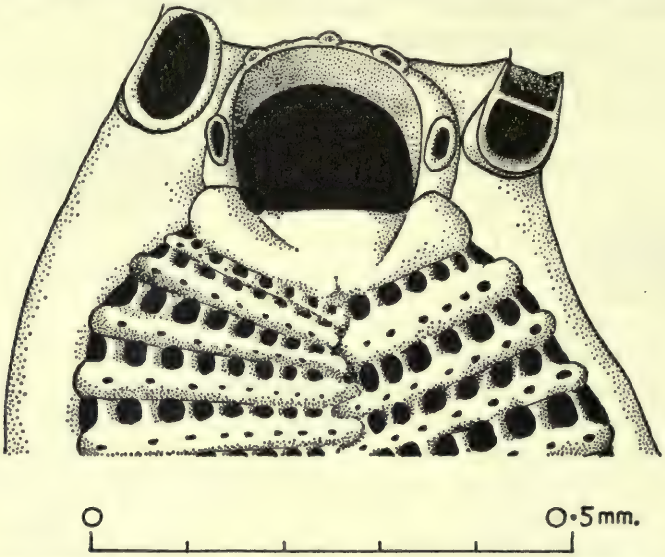


FIG. 110. *Castanopora glandulosa* Lang, D.15009. Holotype. Distal half of adult zooecium with five oral spines and paired, distally pointed and directed avicularia : that on the left is worn, that on the right is broken at its distal end.

STRATIGRAPHICAL DISTRIBUTION. Probably boreal Maastrichtian.

SPECIMEN. D.15009. Holotype—see above.

11. *Castanopora aviculosa* (Lang)

(Pl. 19, fig. 3 : Text-fig. 111).

1916*a* *Rhiniopora aviculosa* Lang, p. 96.
1922 *Rhiniopora aviculosa* Lang : Lang, p. 184, text-fig. 58.
1929 *Rhiniopora aviculosa* Lang : Lang, p. 438, text-fig. 39 (19).
1930 *Rhiniopora aviculosa* Lang : Voigt, p. 551.

HOLOTYPE. In the Collection of Mons. F. Canu. Photograph in the British Museum (Natural History). Maastrichtian ; Maastricht, Limbourg, Holland.

EMENDED DIAGNOSIS. *Castanopora* with 24–26 costae ; avicularia proximally directed, paired, placed distal-laterally, elongate with sharply pointed rostra.

DESCRIPTION. *Zoarium* unilaminar, encrusting or erect. *Zooecia* broadly oval. *Orifice* evenly rounded distally and laterally, proximal margin straight, with distinct, pointed, proximal-lateral constrictions. *Oral spine-bases* of uncertain number, but at least 4, somewhat enlarged. *Frontal shield* flatly arched, variable in length. *Costae* 24–26, each generally with 6, occasionally 7 *lateral costal fusions*. *Outermost intercostal spaces* slot-like and narrow. *Apertural bar* not very wide, form obscure, but probably triangular. *Gymnocyst* not clearly visible, largely obscured by the avicularia ; the zooecia are, however, well spaced : little or no *interzooecial secondary tissue*.

Avicularia of one form : all proximally directed, paired near the distal-lateral margins of the orifice ; other occasional, similar, sporadic forms may occur : a *transverse bar* divides a small, semicircular, proximal portion from a large, elongate, sharply pointed, triangular *rostrum*. *Ovicells* not seen.

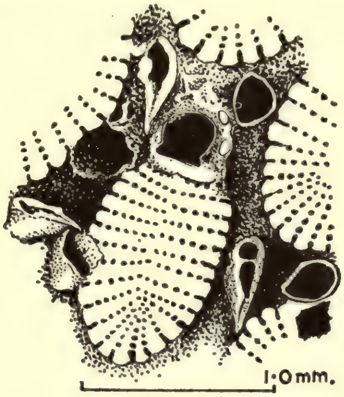


FIG. 111. *Castanopora aviculosa* Lang. Drawing from the photograph reproduced in Pl. 17, fig. 6. Scale approximate.

MEASUREMENTS. (According to Lang, 1922 : 184.)
Zooecia Lz = 1·25 to 1·50 mm.
(No other measurements available.)

REMARKS. Lang's figure and description of *Rhiniopora aviculosa* (1922 : 184, text-fig. 58), based on photographs of the holotype, are misleading. These photographs are not sufficiently clear to show the exact number of oral spine-bases. In MS. notes on the photographs Lang refers to 6 oral spines as present but remarks " sometimes five ". He referred also to dimorphic avicularia " consisting of those with a very long and sharp rostrum, and those whose rostrum is comparatively short and not so sharp ; the former are numerous, sporadically distributed, variously, but generally proximally, directed ; the latter are more numerous, sporadically distributed, and probably always proximally directed ". All the definitely pointed, elongate avicularia visible in the photographs are proximally directed ; the broken and worn bases of this type are the " comparatively short and not so sharp " avicularia of Lang. The avicularia are distinctly paired, with only occasional, sporadic forms.

Nowhere are condyles visible in the broken avicularian apertures. A transverse bar is visible in one complete, pointed avicularium, and the lateral constrictions visible in other elongate avicularia are the broken remains of such transverse bars.

Rhiniopora aviculosa Lang is here regarded as a species of *Castanopora* characterized by proximally directed and pointed avicularia throughout the zoarium.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian.

SPECIMENS. None in the collections—only photographs of part of the holotype zoarium.

12. ***Castanopora magnifica*** (d'Orbigny)

(Pl. 18, figs. 2–7 ; Pl. 19, figs. 1, 2, 4–6 ; Pl. 20, fig. 1 ; Text-figs. 112–116)

1851 *Escharipora magnifica* d'Orbigny, pl. 686, figs. 1–5.
1852 *Escharipora pretiosa* d'Orbigny, pp. 227, 235 ; 1854, p. 1097.
1860 *Escharipora pretiosa* d'Orbigny : Coquand, p. 181.
1865 *Escharipora pretiosa* d'Orbigny : Ubaghs, p. 51.
1887 *Cribilina asperula* Marsson, pp. 97, 109, pl. 10, fig. 8.
1890 *Cribrilina asperula* Marsson : Osswald, p. 108.
1895 *Cribillina* [*sic*] *asperula* Marsson : Deecke, p. 79.
1895 *Cribrillina* [*sic*] *asperula* Marsson : Deecke, p. 87.
1900*b* *Cribrilina asperula* Marsson : Canu, p. 445.
1900*b* *Cribrilina magnifica* (d'Orbigny) : Canu, p. 447.
1913 *Cribrilina cacus* Brydone, p. 437, pl. 14, figs. 6–8.
1916*a* *Castanopora magnifica* (d'Orbigny) Lang, pp. 94, 95.
1916*a* *Rhiniopora aspera* Lang, pp. 96, 97.
1916*a* *Rhiniopora asperula* (Marsson) Lang, pp. 96, 97.
1916*a* *Rhiniopora cacus* (Brydone) Lang, pp. 96, 97.
1916*a* *Rhiniopora horrida* Lang, pp. 96, 97.
1917 *Rhiniopora aspera* Lang : Lang, p. 172.
1922 *Rhiniopora aspera* Lang : Lang, p. 118, pl. 4, fig. 4 ; text-fig. 59.
1922 *Rhiniopora asperula* (Marsson) : Lang, p. 190, pl. 4, fig. 5 ; text-fig. 60.
1922 *Rhiniopora cacus* (Brydone) : Lang, p. 193.
1922 *Rhiniopora horrida* Lang : Lang, p. 194, pl. 4, fig. 6 ; text-fig. 61.
1922 *Castanopora magnifica* (d'Orbigny) : Lang, p. 212.
1925 *Cribrilina asperula* Marsson : Levinsen, p. 376.
1925*c* *Cribrilina asperula* Marsson : Voigt, p. 176.
1929 *Rhiniopora aspera* Lang : Brydone, p. 13.
1929 *Rhiniopora asperula* (Marsson) : Lang, p. 438, text-fig. 39 (20).
1929 *Rhiniopora horrida* Lang : Lang, p. 438, text-fig. 39 (21).
1930 *Rhiniopora cacus* (Brydone) : Voigt, pp. 511, 543, 561, pl. 31, fig. 3.
1930 *Rhiniopora aspera* Lang : Voigt, p. 511.
1930 *Rhiniopora asperula* (Marsson) : Voigt, pp. 511, 543, 561.
1930 *Rhiniopora horrida* Lang : Voigt, pp. 511, 561, pl. 31, fig. 5.
1935 *Rhiniopora aspera* Lang : Bassler, p. 190.
?1940 *Cribrilina magnifica* (d'Orbigny) : Gillard, p. 15.
1953 *Rhiniopora aspera* Lang : Bassler, p. G193, text-fig. 144, 25.
1953 *Rhiniopora aspera* Lang : Illies, pp. 76, 91, 94.
1953 *Rhiniopora asperula* (Marsson) : Illies, p. 97.
1953 *Rhiniopora cacus* (Brydone) : Illies, pp. 76–101, pl. 15, figs. 1–6, pl. 16, figs. 1–2.

LECTOTYPE. (Chosen by Lang, 1922 : 212.) The specimen figured by d'Orbigny, 1851, pl. 686, fig. 2. Maastrichtian of Sainte-Colombe (Manche), and Royan (Charente Inférieure). d'Orbigny Collection.

EMENDED DIAGNOSIS. *Castanopora* with relatively large orifice ; oral spine-bases 4 or 5 ; costae 14–30 (often about 20), each with 4–8 (often 5–7) lateral costal fusions and pelmatidia ; avicularia oblique, proximally directed, occasional, sporadic, somewhat variable in size, rounded.

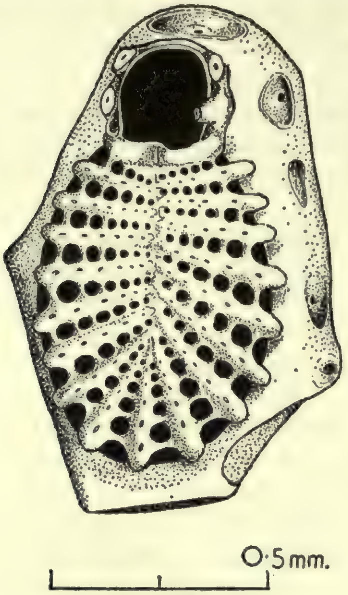
DESCRIPTION. *Zoarium* encrusting or erect, unilaminar. *Zooecia* oval, large. *Orifice* may be wider than high, or of equal height and width, relatively large, evenly rounded distally, sides approximately straight and slightly converging proximally, proximal margin straight, slight proximal-lateral constrictions may be present. *Oral spine-bases* generally 4, less frequently 5, the lateral pair more thickened than the distal pair, a fifth, slender, median, distal oral spine may be present. Where only 4 oral spines are present there is seldom enough space between the distal pair for another single oral spine to develop. *Frontal shield* generally flatly arched. *Costae* of very variable number (from 14 to 30 according to Illies, 1953). In the specimens examined the range was found to be from 14 to 24, taking account of adult individuals only. Each costa generally bears from 4 to 8 (commonly 5–7) *lateral costal fusions* and *pelmatidia*, but there are fewer on the shorter costae close to the apertural bar. *Outermost intercostal spaces* more rounded than slot-like. *Apertural bar* prominent, not very wide, but thickened, especially near the outer ends ; a median ridge is present on the apertural bar and it tends to be prolonged on the frontal shield as an irregular, slight, median ridge producing a narrow median area of fusion. *Gymnocyst* more prominently exposed proximally to the frontal shield than on its lateral margins, not concealed by *interzooecial secondary tissue*. *Communication pores* are seen as two or three shallow, circular depressions in the lateral walls of some zooecia, and as single, larger depressions in the proximal and distal walls, the centre of each depression being perforated by a small, round pore.

Avicularia of one kind : of variable size and occurrence, approximately twice as long as wide, prominent, fairly frequent, proximally directed, oblique, divided by a *transverse bar* into a somewhat smaller proximal portion and a larger, rounded or slightly pointed *rostrum*. Their appearance alters considerably with the degree of wear.

Ovicells rare, hyperstomial, prominent, large, globular, overlapping on to the proximal part of the frontal shield of the distally adjacent zooecium. Each bears two ridges, which converge distally at the mid-line from the proximal-lateral corners. The lateral pair of oral spines may flank the opening of the ovicell.

MEASUREMENTS. *Zooecia* Lz = 0·75 to 1·48 mm.
lz = 0·45 to 1·20 mm.
hr = 0·15 to 0·33 mm.
lr = 0·15 to 0·30 mm.
Avicularia Lz = 0·17 to 0·25 mm.
lz = 0·09 to 0·18 mm.

The highest values of length and breadth given by Illies (1953) are Lz = 1·80 mm.



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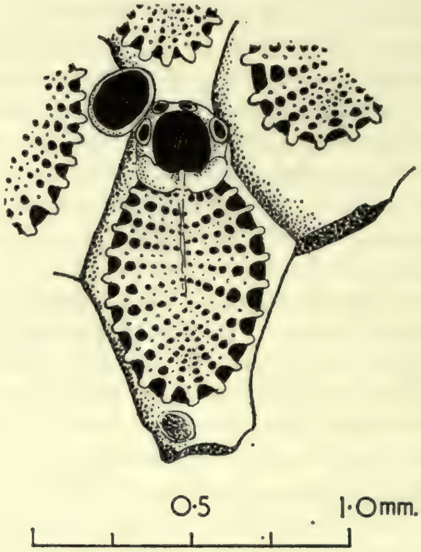

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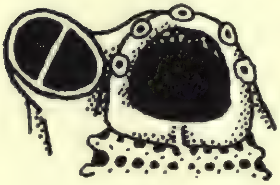
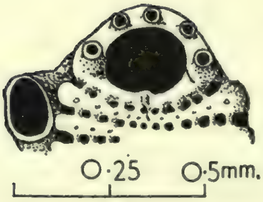


Scale as for Fig. 112



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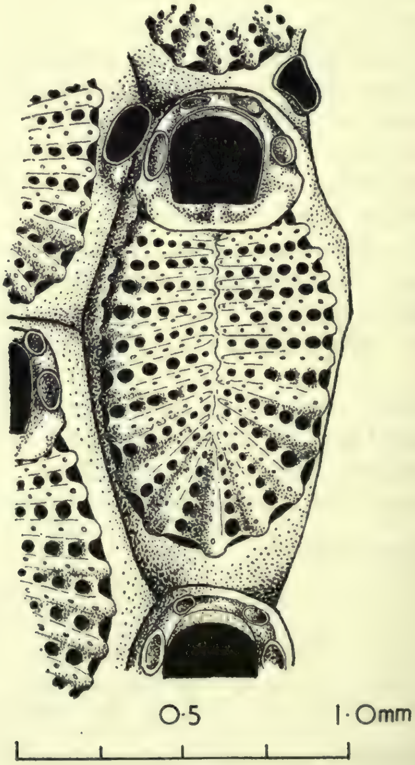

116

and lz = 1·7 mm. These unusually high values possibly include measurement of abnormally long and wide zooecia which occur occasionally in this species.

REMARKS. Voigt (1930 : 511) regarded a free specimen, which he assigned to Marsson's species *asperula*, as synonymous with *Rhiniopora aspera* Lang. Marsson (1887 : 97) originally included both free and encrusting forms in his species *Cribrilina asperula.*

Lang (1922 : 192) suggested that Marsson's encrusting specimens were *Rhiniopora aspera* which was distinguished by Lang from *R. asperula* by its supposedly different growth habit, its slightly greater number of costae, and the occurrence in *R. aspera* of " generally five but occasionally only four " oral spine-bases compared with " 4 considerably thickened " oral spine-bases in *R. asperula.* In the present re-examination of the specimens named *R. aspera* by Lang, it was found that 4 oral spine-bases, rather than 5, are more frequently present. The range in number of costae was given by Lang as 18–20 for *R. aspera* and 20–24 for *R. asperula.*

Only one specimen (D.14176) labelled by Lang " *R. asperula* (Marsson) " is available : 4 oral spine-bases are present and the range in number of costae is 19–22. In the re-examined specimens labelled " *R. aspera* " the range in number of costae is 14–20. Thus the differences between the species are very slight and it is difficult to separate them.

Recently (1953), a statistical variation-study of 40 zoaria of a species placed in *Rhiniopora* [*R. cacus* (Brydone)], from the Maastrichtian of Hemmoor, Germany, has been carried out by Illies. This careful analysis of characters which can be studied quantitatively (those which can be measured or counted) has shown in particular that the number of costae in each frontal shield varies widely, both between individuals of the same colony and individuals of separate zoaria. If anything, the length and breadth measurements of zooecia show the least variation.

Illies (1953 : 99) summarized her work as follows : " 40 colonies of the bryozoan *Rhiniopora cacus* (Brydone) from the chalk of the Maastrichtian of Hemmoor (Niederelbe) were investigated by variation-statistical methods.

" In the first section, the variation of quantitative characters within a single

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FIGS. 112–116. *Castanopora magnifica* (d'Orbigny).

(112) D.31630. A very well-preserved single adult zooecium. Distal and lateral communication pores are well displayed.

(113) D.15620. Holotype of *Rhiniopora aspera* Lang. Distal end of adult zooecium with five oral spines and large oval avicularium with narrow transverse bar.

(114) D.14176. Labelled by Lang " *Rhiniopora asperula* (Marsson) ". Adult zooecium and parts of three distally adjacent zooecia and one worn, oval avicularium. The gymnocyst is typically widely exposed.

(115) N.C.M.76.937 (25/1). Distal end of adult zooecium with five oral spines and worn oval avicularium.

(116) D. 15591*d*. One of five fragments of the same zoarium labelled by Lang " *Rhiniopora cacus* (Brydone) ". Adult zooecium, parts of four adjacent zooecia and two worn, interzooecial avicularia.

colony are examined. From this, it can be shown that a number of characters in the central area of the zoarium vary differently from the characters in the younger (outer) zones. Whereas length-breadth measurements increase in value and lateral costal fusions, costae etc. increase in number in the first four growth-rings, they remain more or less constant in the outer rings.

" The comparison of several zoaria—in the second section—based on the outer rings only, gave wider limits to the variations than has previously been acknowledged. The number of costae varies greatly, so that their taxonomic importance must now be regarded as less than that of the length and breadth measurements—which are seen to be of the greatest value " [translation].

In a preceding section on the limits of variation of the species, Illies listed the extremes of length-breadth measurements of zooecia and the following characters :

Lateral costal fusions	4–8, mainly 5–7.
Form of orifice	Normal, subcircular or super-normal[1] (the last form being found in all colonies).
Oral spines	Some colonies always with 5, others with 4–5.
Apertural bar	Possesses lateral " swellings " of varying strength in different colonies.
Gymnocyst	Varies in breadth.
Avicularia	Vary from 5 to 66 per 100 zooecia.
Median area of fusion	May be " rib-like ", flattened, or not particularly distinct.
Length-breadth ratio	Varies considerably . . . indicating irregular growth.
Ovicells	Rare, those found, all developed to the same degree.

[1] Lang, 1921, p. xlvii, and p. 34 here.

Except for the statements on avicularia and ovicells this revision is confirmed by an examination of the material available in the British Museum (Natural History) and other collections mentioned.

Illies (p. 97) referred to Voigt's (1930) suggestion of re-combining *Rhiniopora aspera* Lang with *R. asperula* (Marsson). In her opinion " such a synonymy is only justified if an encrusting form of *asperula* is also found with, apart from the same measurements, less than twenty costae and with thin oral spines. The statistical investigation of variation in *R. cacus* (Brydone) has shown, however, that the variation of definitive characters is far greater than was previously recognised in the literature, so that it may be presumed that in a similar investigation of *R. aspera* and *R. asperula* the present limits are like-wise found to be too narrow and a merging of *aspera*—and even *cacus*—to *asperula* may be necessary " [translation].

It is apparent that for *R. cacus* the results gained from more usual combined qualitative and quantitative investigations are very similar to those achieved by a statistical study of those characters which may be measured or counted.

In the material examined here Illies' revision of the characters of *R. cacus* is confirmed, and this species is regarded as synonymous with *Rhiniopora aspera* Lang, in its turn a growth form of *Rhiniopora asperula* (Marsson). *R. horrida* is, as stated by Lang (1922 : 194), like *R. cacus*, except for its growth habit, and is also, therefore, included in the synonymy.

But *R. asperula is itself a junior synonym of Castanopora magnifica* (d'Orbigny). Mons. E. Buge has kindly provided a photograph (Pl. 20, fig. 1) [by Mons. P. Mémin of the Serv. Photo. Géol., E.N.S.] of the holotype (?) of d'Orbigny's species as well as the following details : " Costules : 24–26, 4 épines orales, aviculaires oraux à bec dirigé vers la partie proximale de la zoécie ". The characters given, as well as those shown in the photograph, clearly justify the synonymy of the species.

Apparent growth habit is not here regarded as of diagnostic value. Accepting this, the ranges in number of costae, lateral costal fusions and the pelmatidia and oral spines of these species (i.e. *Castanopora magnifica, Rhiniopora asperula, R. aspera, R. cacus, R. horrida*) all overlap, or are similar, and are contained within the limits established by Illies on statistical evidence for *R. cacus*. Qualitative characters, such as degree of arching of the frontal shield, shape and arrangement of avicularia, and width of exposed gymnocyst, all appear to vary within the same relatively wide limits, both in zooecia of the same colony and between zooecia of separate colonies.

The following specimens (labelled by Lang as *Rhiniopora aspera*) have been re-examined ; they include the holotype and 5 paratypes of this species and are here assigned to *Castanopora magnifica* (d'Orbigny).

In D.15620 the better preserved zooecia were measured, Lz ranges from 0·78 to 0·90 mm., lz from 0·45 to 0·50 mm. ; the range in number of costae varies from 14 to 16 and the number of lateral costal fusions varies from 4 to 6, oral spine-bases generally number 4, infrequently 5 may be present. In D.14153, D.14210, D.15383, D.16675 and D.16677—all from Rügen—the range in number of costae is 15–20. D.14210 and D.16677 have well exposed gymnocysts. In these specimens only 4 oral spine-bases are developed on each zooecium ; compared with those of D.15620 these are all slightly thickened. D.15302 and D.15324, also from Rügen, are very badly damaged and worn.

D.31630 is a well-preserved zooecium not included in Lang's 1922 Catalogue. Seventeen costae are present, each with 5 lateral costal fusions and pelmatidia ; there are 4 oral spine-bases. The lateral, proximal and distal walls are completely exposed displaying communication pores. The dimensions of the zooecium are : Lz = 1·15 mm., lz = 0·66 mm., hr = 0·24 mm., lr = 0·21 mm.

The holotype of *Rhiniopora horrida* Lang, D.14171, possesses only four whole zooecia, each with four oral spine-bases, the lateral pair in each case being thicker than the distal pair, a condition common in the other specimens here referred to *Castanopora magnifica* (d'Orbigny). All the oral spine-bases in D.14171 tend to be slender, and the zooecia are generally less robust than in the encrusting forms, probably reflecting the growth habit (cf. p. 22 for remarks on the growth habit of *Steganoporella buski* Harmer). The range in number of costae in D.14171 is 19–21 with 5–6 lateral costal fusions on each costa. D.15020 is much broken and very worn. The zooecia are over 1·00 mm. long. It is not possible to determine the specific characters, and its placing, by Lang, in this species is very doubtful.

D.15591 *a–e*, labelled by Lang as *R. cacus* (Brydone), is an imperfectly preserved, fragmented zoarium encrusting five pieces of echinoid test. In fragment *b* three abnormal zooecia are present, two being very wide and one unusually long. The measurement of zooecia such as these may account for the somewhat high values recorded by Illies for *R. cacus*. Several zooecia in fragment *a* possess broken ovicells.

Poorly preserved avicularia are present in D.15591, D.14167 and D.16676—the last two are specimens from Rügen also labelled by Lang as *R. cacus*.

Four specimens from the Norwich Castle Museum collections—N.C.M.2194 (3), 76.937 (25/1), 76.937 (26/1) and 112.22 (1/1)—belong to *Castanopora magnifica* (d'Orbigny). The range in number of costae is 16–21, with 4, occasionally 5, oral spine-bases and from 4 to 6 lateral costal fusions and pelmatidia on each costa. N.C.M.76.937 (26/1) has less thickened oral spine-bases than is usual.

A very well preserved zoarial fragment, D.40673, encrusting a piece of echinoid test, from a recently exposed outcrop of the *O. lunata* Chalk at Mundesley, Norfolk, is also assigned to *Castanopora magnifica* (d'Orbigny).

In addition, the three zoarial fragments figured by Brydone (1913 : 437, pl. 14, figs. 6–8) as *Cribrilina cacus* have been re-examined. S.M., B.36264, that shown in fig. 6, was placed by Lang (1922 : 188) in *Rhiniopora aspera*. S.M., B.36265 (fig. 7 of Brydone) was chosen by Lang (p. 193) as lectotype of *Rhiniopora cacus* (Brydone), to which species Lang also assigned S.M., B.36266 (fig. 8 of Brydone). These specimens all belong to *Castanopora magnifica* (d'Orbigny) ; their dimensions and other details are as follows :

Zooecia Lz = 1·18 to 1·45 mm.
lz = 0·68 to 1·20 mm.
hr = 0·25 to 0·31 mm.
lr = 0·22 to 0·30 mm.
Costae 20–24.
Lateral costal fusions 5–8.
Oral spine-bases 4 or 5.
Avicularia Lz = 0·17 to 0·25 mm.
lz = 0·10 to 0·18 mm.

It is evident that the specimens are generally larger than most of the material which is here assigned to *C. magnifica* (d'Orbigny) ; they all, however, fall well within the limits of variation established by Illies (1953) and confirmed here by qualitative as well as quantitative study.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *Belemnitella mucronata*, and Maastrichtian, zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk).

SPECIMENS. D.15620. Zoarial fragment. Holotype of *Rhiniopora aspera* Lang. Maastrichtian, zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk). Trimingham, Norfolk. A. C. Savin Collection.

D.14153, D.14210, D.15383, D.16675, D.16677. Five paratypes of *Rhiniopora aspera* Lang. Zoarial fragments encrusting pieces of echinoid test. Horizon given as " Senonian, zone of *B. mucronata* ", but probably boreal Maastrichtian. Rügen. Agnes Laur Collection.

D.14171. Holotype of *Rhiniopora horrida* Lang. Small zoarial fragment. Horizon locality and collection as for D.14153.

D.14176. Zoarial fragment labelled by Lang " *Rhiniopora asperula* (Marsson) ". Horizon, locality and collection as for D.14153.

D.15020. Very worn and damaged zoarial fragment labelled by Lang " *Rhiniopora horrida* ". Horizon, locality and collection as for D.14153.

D.15302, D.15324. Broken and worn fragments of two zoaria labelled " *Rhiniopora aspera* Lang ". Horizon, locality and collection as for D.14153.

D.15591*a–e*. Five fragments of the same zoarium encrusting pieces of echinoid test. Horizon, locality and collection as for D.15620. The specimen was labelled by Lang " *Rhiniopora cacus* (Brydone) ".

D.14167, D.16676. Two small zoarial fragments labelled by Lang " *Rhiniopora cacus* (Brydone) ". Horizon, locality and collection as for D.14153.

D.31630. A well-preserved single zooecium. Senonian, zone of *B. mucronata*. Norwich, Norfolk. T. H. Withers Collection.

D.31707. Small zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Pit a quarter mile south-south-west of Coltishall, Norfolk. T. H. Withers Collection.

D.40673. Zoarial fragment encrusting a piece of echinoid test. Maastrichtian, zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk). Exposed on foreshore, 1954, 100 yards south of the Kiln Camping Site, Mundesley, Norfolk. D. R. Howlett Collection.

OTHER MATERIAL. N.C.M.76.937 (25/1). Incomplete zoarium encrusting a whole test of *Cardiaster ananchytis* Leske. Senonian, zone of *B. mucronata*. Catton, near Norwich, Norfolk. R. M. Brydone Collection.

N.C.M.2194(3). Incomplete zoarium encrusting a whole echinoid test labelled " *Epiaster gibba* S. Woodward ". Senonian, zone of *B. mucronata*. Collection unknown.

N.C.M.76.937(26/1). Zoarial fragment encrusting a whole test of *Cardiaster ananchytis* Leske. Senonian, zone of *B. mucronata*. Harford, near Norwich, Norfolk. R. M. Brydone Collection.

N.C.M.112.22(1/1). Incomplete zoarium encrusting a whole echinoid test labelled " *Galerites vulgaris* Lam.". Senonian, zone of *B. mucronata*. Thorpe-next-Norwich, Norfolk. Collection unknown.

S.M., B.36264–66. Three well-preserved zoarial fragments encrusting pieces of echinoid test. Maastrichtian, zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk). Trimingham, Norfolk. R. M. Brydone Collection.

S.M., B.36264—part of this specimen was figured by Brydone (1913 : 437, pl. 14, fig. 6) as *Cribrilina cacus*. Lang (1922 : 188) tentatively assigned the specimen to *Rhiniopora aspera*.

S.M., B.36265—part of this specimen was figured by Brydone (1913 : 437, pl. 14, fig. 7) as *Cribrilina cacus*. Lang (1922 : 193) chose it as lectotype of *Rhiniopora cacus* (Brydone).

S.M., B.36266—part of this specimen was figured by Brydone (1913 : 437, pl. 14, fig. 8) as *Cribrilina cacus*. Lang (1922 : 193) assigned it to *Rhiniopora cacus*.

13. ***Castanopora faujasi*** (von Hagenow)

1851 *Cellepora* (? *Dermatopora*) *faujasi* von Hagenow, p. 99, pl. 10, fig. 19*a*, *b* [the question-mark is omitted on p. 99].

1930 *Rhiniopora faujasi* (von Hagenow) Voigt, p. 511, pl. 31, fig. 2.

EMENDED DIAGNOSIS. *Castanopora* with orifice wider than high ; Lz about 1·00 mm., lz about 0·60 mm. ; costae 13–15, each with 6–7 lateral costal fusions ; gymnocyst widely exposed ; apparently no avicularia.

REMARKS. Von Hagenow's figure of this species (1851, pl. 10, fig. 19*b*) shows only broken zooecia lacking frontal shields. But the shape of the broken apertures strongly suggests a cribrimorph, with well-spaced zooecia which had wide orifices. Von Hagenow described the zoarium as a series of " quincuncially arranged cells with transversely oval, almost round, apertures, each with a semicircular emargination " [translation]. This " emargination " is undoubtedly the orifice lacking its proximal border, and it is thus an apparent continuity with the worn aperture of the zooecium.

Voigt (1930 : 511) assigned a specimen to the species ; complete frontal shields are present and it is clearly a *Castanopora*. Apart from the characters mentioned in the above diagnosis it is not possible to interpret other details from the figure or from Voigt's note on the specimen.

STRATIGRAPHICAL DISTRIBUTION. Horizon given as " Senonian, upper part of zone of *B. mucronata* ", but very probably Maastrichtian (Maastricht, Holland).

SPECIMENS. None in the collection.

14. ***Castanopora voigti***[1] sp. nov.

1930 *Rhiniopora* cf. *hispida* Lang : Voigt, pp. 511, 561, pl. 31, fig. 6.

HOLOTYPE. The specimen figured by Voigt, 1930, pl. 31, fig. 6. Horizon given as " Senonian, upper part of zone of *B. mucronata*, Møen ", but since shown to be Maastrichtian, zone of *Belemnella lanceolata* (see below).

DIAGNOSIS. *Castanopora* with erect, cylindro-quadrate zoarium ; zooecia of the 4 adjacent rows alternate ; orifice higher than wide ; costae 20–25.

DESCRIPTION. (Based on Voigt's figure.) *Zoarium* erect, cylindro-quadrate, composed of 4 adjacent rows of alternating zooecia. *Zooecia* oval or rectangular. *Orifice* higher than wide, evenly rounded distally and laterally, proximal margin straight. *Oral spine-bases* of uncertain number, at least two pairs present. *Frontal shield* oval, very flatly arched, descending sharply near the outer ends of the costae. *Costae* 20–25, each with 4, possibly at least 5 *lateral costal fusions*. *Apertural bar* not very wide, slightly curved proximally. *Gymnocyst* well exposed, especially proximally to the frontal shield. *Avicularia* and *ovicells* not shown in the figure.

MEASUREMENTS. (According to Voigt.)
Zooecia Lz = 0·75 to 0·80 up to 1·00 mm.

REMARKS. Voigt (1930 : 511, pl. 31, fig. 6) briefly described a specimen from the same horizon as the holotype of *Rhiniopora hispida* Lang, but he only compared it with that species in view of the uncertainty of the characters given by Lang. *R. hispida* was founded on an extremely worn and badly damaged specimen (D.14996), in which all the frontal shields are missing except for a fragment of one. The characters given by Lang are largely hypothetical as he himself indicated by placing most of them in square brackets, a usage which he reserved for conjectural and uncertain statements. The name *Rhiniopora hispida* must therefore be discarded since the species cannot be satisfactorily defined.

---

[1] After Prof. Ehrhard Voigt.

C. voigti is distinguished from all other known species of *Castanopora* by its cylindro-quadrate zoarium. Further material may show the presence of avicularia and the number of oral spine-bases.

Voigt (in a letter dated 16th June, 1952) has indicated that the chalk of Møen, the locality of the holotype, is of Maastrichtian age belonging to the zone of *Belemnella lanceolata*. Lang (1921 : lxxxiv) had regarded the Møen chalk as Danian, and Voigt (1930 : 511) had originally placed it as Senonian, uppermost part of the zone of *Belemnitella mucronata*.

Stratigraphical distribution. Maastrichtian, zone of *Belemnella lanceolata*.

Specimens. None in the collection.

Species of Uncertain Systematic Position Previously Assigned to *RHINIOPORA* and *CASTANOPORA*

(1) ***Cellepora perforata*** Quenstedt

1879 *Cellepora perforata* Quenstedt, p. 312, pl. 154, fig. 37.

Remarks. Lang (1922 : 183) referred this species to *Rhiniopora*, but from Quenstedt's original description and figure it is possible to deduce only that the specimen was an encrusting cribrimorph with hyperstomial ovicells. It cannot be assigned with any certainty at all to *Castanopora* or any other genus, even though its horizon is recorded as Maastrichtian of Maastricht.

(2) ***Reptescharella radiata*** d'Orbigny

1852 *Reptescharella radiata* d'Orbigny, pl. 716, figs. 4–6.
1853 *Reptescharella radiata* d'Orbigny : d'Orbigny, p. 468.

Remarks. Lang placed this species in *Rhiniopora*. In the original description of *Reptescharella radiata* d'Orbigny (1853 : 468) referred to the encrusting habit of the species and to the presence of 16 costae, and the orifice was described as " ovale, transverse " suggesting that lr exceeds hr in value. Further interpretation of the species must rest on d'Orbigny's figures (1852, pl. 716, figs. 4–6), which, however, are highly stylized ; no avicularia are shown, and the zooecia are closely placed with 16–18 costae each with 5–7 lateral costal fusions. The orifices are about twice as wide as high.

Without information on the nature of the oral spines, the avicularia and other details, it is not possible to state with certainty that the species belongs to *Castanopora*. The recorded horizon, Campanian and Santonian, is lower than for most species of *Castanopora*.

(3) ***Rhiniopora hispida*** Lang

1916*a* *Rhiniopora hispida* Lang, pp. 96, 97.

This species has been discussed on p. 236 under the remarks on *Castanopora voigti* sp. nov.

(4) ***Repteschariopora ornata*** d'Orbigny

1852 *Repteschariopora ornata* d'Orbigny, pl. 720, figs. 6–8.
1853 *Repteschariopora ornata* d'Orbigny : d'Orbigny, p. 494.
1854 *Repteschariopora ornata* d'Orbigny : d'Orbigny, p. 1098.

Holotype. d'Orbigny Collection, No. 8012, Laboratoire de Paléontologie, Muséum National d'Histoire naturelle, Paris. Senonian. Vendôme, (Loir et Cher), France.

Remarks. Lang (1916*a* : 94 ; 1922 : 213) placed this species in *Castanopora*. Dr. E. Buge has kindly provided me with a photograph (by Mons. P. Mémin of the Serv. Photo. Géol. E.N.S.) of the holotype and details of its preservation. In a letter (8th December, 1954) he stated, " Costules nombreuses, mais presque indiscernables sur le spécimen. Epines non distinctes (probablement détruites). Aviculaires oraux (?) érodés, non définissables ".

The recorded horizon, Senonian [Santonian] of Vendôme, Loir et Cher, is again lower than for most species of *Castanopora* and it is most uncertain that the species belongs to that genus.

Genus ***UBAGHSIA*** Jullien

1826 *Celepora* : Goldfuss, pp. 26, 248 [*partim*].
1828 *Cellepora* : Morren, p. 34 [*partim*].
1832 *Cellepora* : Dumont, p. 360 [*partim*].
1834 *Cellepora* : von Klöden, pp. 264, 341 [*partim*].
1836 *Discopora* : Edwards, p. 248 [*partim*].
1840 *non Eschardoides* : Roemer, p. 14.
1846 *Cellepora* : Geinitz, p. 609 [*partim*].
1848 *Cellepora* : Bronn, p. 253 [*partim*].
1848 *Discopora* : Bronn, pp. 255, 431 [*partim*].
1849 *Discopora* : Bronn, p. 130 [*partim*].
1849 *Cellepora* : Geinitz, p. 248 [*partim*].
1850 *Escharina* : d'Orbigny, p. 262 [*partim*].
?1851 *Cellepora* (*Discopora*) : von Hagenow, p. 96 [*partim*].
1851 *Cellepora* (*Dermatopora*) : von Hagenow, p. 98 [*partim*].
1851 *Cellepora* (*Dermatopora*) : Bronn & Roemer, p. 102 [*partim*].
?1852 *Reptescharella* d'Orbigny, pls. 604, 715–716 [*partim*].
?1852 *Semiescharipora* d'Orbigny, pls. 717–719 [*partim*].
?1852 *Reptecharipora* d'Orbigny, pls. 719–720 [*partim*].
?1853 *Reptescharella* : d'Orbigny, p. 464 [*partim*].
?1853 *Semiescharipora* : d'Orbigny, p. 479 [*partim*].
?1853 *Repteschariopora* : d'Orbigny, p. 489 [*partim*].
?1854 *Semiescharipora* : d'Orbigny, p. 1097 [*partim*].
?1854 *Repteschariopora* : d'Orbigny, p. 1098 [*partim*].
?1857 *Reptescharella* : Pictet, p. 110 [*partim*].
?1857 *Semiescharipora* : Pictet, p. 112 [*partim*].

?1860 *Semiescharipora* : Coquand, p. 183.
1862 *Cellepora* : Goldfuss, p. 24 [*partim*].
1865 *Steginopora* : Ubaghs, p. 55.
1879 *Cellepora* : Quenstedt, p. 303 [*partim*].
1879 *Semiescharipora* : Ubaghs, p. 217 [*partim*].
?1879 *Lepralia* : Ubaghs, p. 221 [*partim*].
1881 *Semiescharipora* : Mourlon, p. 116 [*partim*].
?1881 *Lepralia* : Mourlon, p. 119 [*partim*].
1885 *Semiescharipora* : Vine, pp. 116, 156 [*partim*].
1885 *Cellepora* : Vine, p. 161 [*partim*].
1885 *Cellepora* (*Dermatopora*) : Vine, p. 164 [*partim*].
?1885 *Cellepora* (*Discopora*) : Vine, p. 164 [*partim*].
1886 *Steginopora* : Jullien, pp. 612, 614 [*partim*—*non S. irregularis* d'Orbigny, ?*non S. aculeata* d'Orbigny, *non S. pulchella* d'Orbigny, ?*non S. ornata* d'Orbigny].
1886 *Ubaghsia* Jullien, pp. 610, 616 [*partim*—*U. reticulata* only].
1887 *Cribrilina* : Marsson, pp. 96, 109 [*partim*].
1889 *Semiesharipora* : Ubaghs, p. 52.
1900*b* *Cribrilina* : Canu, p. 445 [*partim*].
1900*b* *Cribrilina* (*Costula*) : Canu, p. 450.
1900*b* *Steginopora* (*Ubaghsia*) : Canu, p. 455 [*partim*—*S.* (*Ubaghsia*) *reticulata* only].
1900*b* *Semiescharipora* : Canu, p. 457 [*partim*].
1900*b* *Reptescharipora* : Canu, p. 457 [*partim*].
1910 *Cribrilina* : Canu, p. 63 [*partim*].
1916*a* *Ubaghsia* : Lang, 93, 99.
1916*a* *Batrachopora* Lang, pp. 101, 110 [*partim*—?*B. ovalis* (d'Orbigny), ?*B. convexa* (d'Orbigny), ?[*B.*] *signata* (von Hagenow), *non B. royanensis* Lang].
?1916*a* *Cellepora* (*Discopora*) : Lang, p. 111.
1919*c* *Batrachopora* : Lang, p. 105.
1919*d* *Batrachopora* : Lang, pp. 192, 197, 199, 203, 208, 217, 223 [*partim*—?*B. ovalis* (d'Orbigny), ?*B. convexa* (d'Orbigny), ?[*B.*] *signata* (von Hagenow), *non B. royanensis* Lang].
?1919*d* *Cellepora* (*Discopora*) : Lang, p. 205.
1920 *Steginopora* : Canu & Bassler, p. 282, fig. 81 S.
1921 *Batrachopora* : Lang, pp. lvii, xc, xci [*partim*].
1921 *Ubaghsia* : Lang, pp. lxvi, xc, xci, xciii.
1922 *Ubaghsia* : Lang, p. 225.
1922 *Batrachopora* : Lang, p.357 [*partim*—?*B. ovalis* (d'Orbigny), ?*B. convexa* (d'Orbigny), ?[*B.*] *signata* (von Hagenow), *non B. royanensis* Lang].
1925 *Cribrilina* : Levinsen, p. 375 [*partim*—*C. brachiata* only].
1925*b* *non Batrachopora* : Voigt, pp. 99, 103.
1925*c* ?*Batrachopora* : Voigt, p. 175.
1927 *Cribrilina* : Voigt, p. 102 [*partim*].
1927 *Ubaghsia* : Canu & Bassler, p. 41.
1927 *Batrachopora* : Canu & Bassler, p. 55.
1929 *Steginopora* : Canu & Bassler, p. 243 [*partim*—*S. ocellata* only].
1929 *Ubaghsia* : Canu & Bassler, p. 244.
1929 *Batrachopora* : Lang, p. 439.
1929 *Ubaghsia* : Lang, p. 439.
1930 *Ubaghsia* : Voigt, pp. 513, 515, 538, 561.
1930 *Batrachopora* : Voigt, pp. 515, 561 [*partim*—*non B. ultima* Voigt].
1935 *Batrachopora* : Bassler, pp. 31, 55.
1935 *Ubaghsia* : Bassler, pp. 31, 222.
1939 *non Batrachopora* : Voigt, p. 93.
?1940 *Cribrilina* : Gillard, p. 15 [*partim*].

1949 *non Batrachopora* [*Escharoides*] : Voigt, pp. 41, 43.
1953 *Batrachopora* : Bassler, p. G192.
1953 *Ubaghsia* : Bassler, p. G193.

TYPE SPECIES. *Steginopora reticulata* Ubaghs, 1865 : 55. Maastrichtian. Ober Bryozoenschichte (horizon *f* of Ubaghs). Valkenburg (Fauquemont), east of Maastricht, or Geulem, north-east of Maastricht, Holland.

EMENDED DIAGNOSIS. Pelmatoporinae with relatively large zooecia ; branched or unbranched distal oral spines ; proximal and distal oral shields present, the latter may be less developed ; the former composed of paired, large, proximal-lateral oral avicularia, raised on stout stalks, united above the secondary orifice and often fused on their distal sides with the distal-lateral oral spines, the distal oral shield less prominent, formed by the enlarged, sometimes branched, often fused, distal oral spines and the upgrowth of secondary calcareous tissue on the rim of the secondary orifice ; apertural bar not involved in the proximal oral shield ; each costa with two or more pelmata ; secondary tissue forming a tertiary front wall, those of adjacent zooecia usually united (the tertiary front wall is frequently destroyed during fossilization) ; interzooecial avicularia may occur.

REMARKS. *Ubaghsia* Jullien and *Batrachopora* Lang were regarded by Lang as distinct genera which he placed in separate subfamilies of the Pelmatoporidae, the former in the Castanoporinae (1922 : 154) and the latter in the Pelmatoporinae (1922 : 235). The two subfamilies are here merged : see remarks on the subfamily Pelmatoporinae.

Neither pelmata nor pelmatidia were indicated in the original figures or descriptions of *Ubaghsia* given by Ubaghs (1865) and Jullien (1886), but other characters, which were clearly shown, are very closely comparable with those of *Batrachopora* Lang.

The diagnoses of *Ubaghsia* and *Batrachopora* given by Lang (1916*a* : 93, 101) and later slightly modified (1922 : 225, 358) show that he distinguished between the genera on the basis that the former possessed pelmatidia and branched distal oral spines, while the latter had pelmata and unbranched distal oral spines. The distinction between pelmata and pelmatidia is not a valid one, nor should the branching of oral spines be considered of generic importance. Further, it is very doubtful whether *Ubaghsia reticulata* has branched spines (cf. Jullien, 1886, pl. 18, fig. 4 ; and Voigt, 1930, pl. 31, fig. 19). Thus *Ubaghsia* and *Batrachopora* are synonymous, as Voigt (1930 : 515) has already suggested might be the case.

In the present revision, all the available material, previously assigned to *Ubaghsia* and *Batrachopora*, has been re-examined, and two new species of *Ubaghsia* are described.

Where specimens have been available, the species have been distinguished on general zooecial and avicularian characters rather than on the form of the oral shields which are mainly of generic significance. The form of the proximal oral shield is very often much modified by wear, but the original presence or absence of this large secondary structure can usually be determined even in well-worn specimens.

Lang (1922 : 358), in his remarks on *Batrachopora*, was concerned principally with the evolutionary relationships of the species which he recognized as belonging to the genus. Several of these species, and others later assigned to *Batrachopora* by Voigt, are of very uncertain systematic position (see p. 264); they are not accepted here as species of *Ubaghsia*.

Jullien (1886 : 614, pls. 17–20) described and figured several species which he assigned to *Steginopora* d'Orbigny, and erected the genus *Ubaghsia* to include *Steginopora reticulata* Ubaghs and a new species, *Ubaghsia arcifera*. Lang (1916*a* : 99, 100; 1922 : 225) regarded all these species as belonging to *Ubaghsia*, with the exception of *U. arcifera* which he placed in *Phrynopora* (Lang, 1916*a* : 97, 98; 1922 : 201). If the species of uncertain systematic position, previously assigned to *Batrachopora*, are excluded from *Ubaghsia*, and if Jullien's species are taken into account, much of Lang's suggested evolution of the genera must also be questioned.

It is possible that *Ubaghsia* Jullien is synonymous with *Disteginopora* d'Orbigny and *Steginopora* d'Orbigny, which apparently differ from one another only in their zoarial growth-habit. The tertiary front wall of *Ubaghsia ocellata* and *U. demorgani* appears to be somewhat similar to that found in *Steginopora ornata* d'Orbigny and *Disteginopora horrida* d'Orbigny. However, it is difficult to interpret species from d'Orbigny's stylized figures and inadequate descriptions. Until the holotypes, or new topotype material, of d'Orbigny's species can be examined it is better to retain *Ubaghsia* Jullien as a separate genus.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zones of *M. cor-anguinum, G.* [*A.*] *quadrata, B. mucronata* and Maastrichtian.

KEY TO THE SPECIES OF *UBAGHSIA* JULLIEN

- (I) *Ubaghsia* with orifice much smaller than the frontal shield.
  - (A) Oral spines unbranched.
    - (1) Avicularia of one kind only—a large oral pair.
      - (*a*) 8–10 costae, each with 3 lateral costal fusions, Lz = 0·70 to 0·80 mm., lz = 0·50 to 0·57 mm., oral avicularia fused above secondary orifice to give a complete proximal oral shield. . 1. ***U. ranunculus*** (Lang)
      - (*b*) 18–22 costae; proximal oral shield apparently incomplete; frontal shield distinctly pointed proximally . . . 2. ***U. aurita*** (Lang)
    - (2) Avicularia of two kinds: (*a*) a large oral pair, (*b*) an interzooecial or vicarious, paired or unpaired, small form.
      - (*a*) Shape of orifice variable: wider than high or of equal height and width.
        - (i) Zooecia larger, 9–10 costae, each with 2 lateral costal fusions; interzooecial avicularia small, rounded, unpaired . 3. ***U. gasteri*** sp. nov.
        - (ii) Zooecia shorter, 7–10 costae, each with 2, more often 3, lateral costal fusions; interzooecial avicularia larger, pointed . 4. ***U. langi*** sp. nov.
      - (*b*) Orifice always wider than high.
        - (i) 7 costae, each with 2, occasionally 3, lateral costal fusions; zooecia over 1·00 mm. long . . . . 5. ***U. crassa*** (Lang)
        - (ii) 10–14 costae, each with 3 or 4 lateral costal fusions.
          - (α) Zooecia over 1·00 mm. long . . . . . 6. ***U. coaxans*** (Lang)
          - (β) Zooecia about 0·73 mm. long . . 7. ***U. perforata*** (Marsson)
  - (B) Oral spines branched.
    - (1) Distal oral spines bifurcate only; tertiary front wall with regular lacunae and a longitudinal, narrow, median depression proximal to each orifice 8. ***U. ocellata*** (Jullien)

(2) Distal oral spines each with 3–6 branches.
    (*a*) Orifice often as wide as high ; tertiary front wall thick and very irregular 9. ***U. meudonensis*** (Jullien)
    (*b*) Orifice wider than high ; transversely elongate-oval or oblong ; tertiary front wall thin, with regularly arranged lacunae and a longitudinal, narrow, median depression proximal to each secondary orifice 10. ***U. demorgani*** (Jullien)

(II) *Ubaghsia* with orifice nearly as large as, or larger than the frontal shield.
    (A) Orifice wider than high (hr = 0·20 to 0·25 mm., lr = 0·26 to 0·35 mm.) ; distal oral spines unbranched, often fused together at base . 11. ***U. reticulata*** (Ubaghs)
    (B) Orifice very large, of equal height and width (hr = 0·40 to 0·42 mm., lr = 0·40 to 0·45 mm.) . . . . 12. ***U. ornata*** (Goldfuss)

The following species, previously assigned to *Batrachopora* Lang, are of uncertain systematic position, and are therefore omitted from the above key. They are discussed on pp. 264–266.

(1) *Cellepora* (*Discopora*) *signata* von Hagenow.
(2) *Semiescharipora ovalis* d'Orbigny.
(3) *Reptescharipora convexa* d'Orbigny.
(4) *Batrachopora royanensis* Lang.
(5) *Batrachopora ultima* Voigt.
(6) *Escharoides peltata* Roemer.

1. ***Ubaghsia ranunculus*** (Lang)

(Pl. 20, fig. 2 ; Text-fig. 117)

1916*a* *Batrachopora ranunculus* Lang, pp. 110, 111.
1919*d* *Batrachopora ranunculus* Lang : Lang, pp. 203, 206, 208, 219, 221, text-figs. 33–35, 81.
1921 *Batrachopora ranunculus* Lang : Lang, pp. lvii, xci.
1922 *Batrachopora ranunculus* Lang : Lang, p. 362, pl. 8, fig. 1 ; text-fig. 114.
1935 *Batrachopora ranunculus* Lang : Bassler, p. 55.
1953 *Batrachopora ranunculus* Lang : Bassler, p. G192, text-fig. 144, 14.

Holotype. D.23388. Small zoarial fragment encrusting part of a *Cidaris* plate. Labelled "*Batrachopora ranunculus* Lang. Upper Senonian, Rügen"—probably boreal Maastrichtian. Agnes Laur Collection.

Emended diagnosis. *Ubaghsia* with zooecia 0·70 to 0·85 mm. long, 0·50 to 0·57 mm. wide ; secondary orifice wider than high (hr = 0·13 to 0·15 mm., lr = 0·20 mm.), much smaller than the frontal shield ; costae 8–10, each with 3 lateral costal fusions and pelmata ; avicularia of one kind only, a relatively large lateral oral pair fused above the secondary orifice to form a prominent proximal shield.

Description. *Zoarium* encrusting, unilaminar. *Zooecia* broadly oval. *Secondary orifice* wider than high, much smaller than the frontal shield, distally rounded, sides and proximal margin straight ; *distal oral shield* indistinct ; *proximal oral shield* prominent, formed by the paired, large, lateral oral avicularia which are raised on stout stalks and connected above the orifice by a bar of calcareous tissue. *Oral spines* probably 4, the distal pair are somewhat enlarged, but not lengthened, and are immersed in the secondary tissue accumulated on the distal rim of the orifice. The distal-lateral pair of oral spines are very probably fused on to the distal sides of the lateral oral avicularia and thus form part of the proximal oral shield. *Frontal shield* flat, except at the margins, broadly oval. *Costae* 8–10, fairly narrow, slightly tapering inwards. Near the outer end of each costa is a *pelma*, proximally to this the costa slopes down steeply to meet the gymnocyst; inwards from this pelma each costa is level and carries two smaller *pelmata*. Other pelmata or pelmatidia have not been seen. Somewhat arcuate *lateral costal fusions* arise at the levels of the pelmata producing fairly regular, somewhat elongate *intercostal spaces*. *Apertural bar* not markedly thickened, but generally wider than the largest costae, flat and straight, with at least two large primary pelmata near either end.

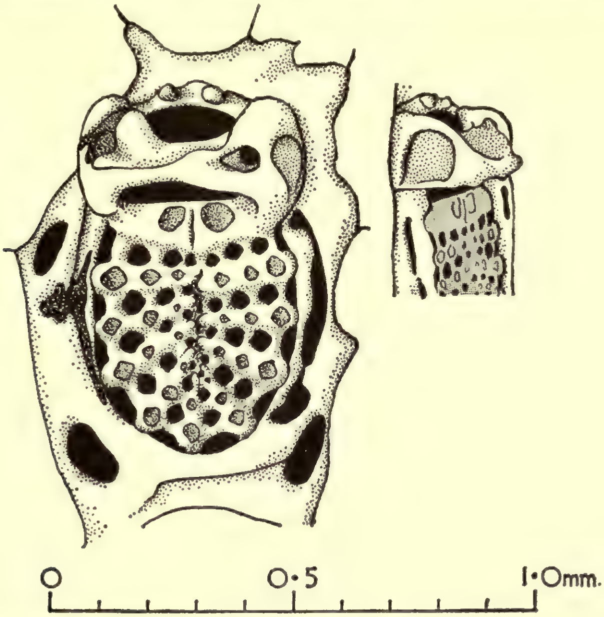

FIG. 117. *Ubaghsia ranunculus* (Lang), D.23388. Holotype. Adult zooecium with complete proximal oral shield.

Gymnocyst smooth, well-exposed proximally to the frontal shield, but often obscured laterally by *interzooecial secondary tissue* which is fairly abundant, in places filling the interzooecial valleys and containing irregularly oval *lacunae*. *Tertiary front wall* not seen, very probably never formed.

Avicularia apparently of one kind only, a large, prominent, lateral oral pair occurring one on either side of, and very close to, the proximal-lateral margins of the secondary orifice. They are raised on stout, much thickened stalks and are joined above the orifice by a bar of calcareous tissue forming a complete proximal oral shield. *Interzooecial avicularia* not seen, very probably absent. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·70 to 0·85 mm.
lz = 0·50 to 0·57 mm.
hr = 0·13 to 0·15 mm.
lr = 0·20 mm.

REMARKS. Only one specimen, D.23388, is available. Lang (1922 : 364) has stated that " occasional, sporadically-distributed aviculoecia [avicularia] appear in the interoecial [interzooecial] secondary tissue ", but they have not been seen. He probably interpreted oval lacunae as avicularia. Nor have " quaternary pelmatidia " been observed. Lang suggested that this species might have been derived from a form resembling *Ubaghsia perforata* (Marsson), but this is very uncertain.

STRATIGRAPHICAL DISTRIBUTION. Probably Maastrichtian.

SPECIMEN. D.23388. Holotype—see above.

2. *Ubaghsia aurita* (Lang)

(Pl. 20, fig. 3)

1916*a* *Batrachopora aurita* Lang, p. 111.
1919*d* *Batrachopora aurita* Lang : Lang, pp. 205, 206.
1922 *Batrachopora aurita* Lang : Lang, p. 376, text-fig. 119.

EMENDED DIAGNOSIS. *Ubaghsia* with zooecia more than twice as long as wide [according to Lang, Lz = about 1·10 mm., lz = about 0·49 mm.] ; secondary orifice wider than high or of equal height and width, much smaller than the frontal shield ; oral spines probably 4 ; frontal shield distinctly pointed proximally ; costae very numerous, 18–22 ; avicularia apparently of one kind only, a large lateral oral pair.

DESCRIPTION. [Based on a photograph of the holotype.] *Zoarium* unilaminar, encrusting [according to Lang]. *Zooecia* fairly closely placed, noticeably elongate. *Secondary orifice* wider than high, or of equal height and width, rounded distally with straight sides which tend to converge somewhat proximally, and a straight proximal margin. *Oral spines* probably 4. It is possible to distinguish, from the photograph, a distal pair of thickened, but not lengthened, oral spines ; distal-lateral oral spines, if present, are probably fused on to the distal sides of the lateral oral avicularia, forming, with these, the *proximal oral shield*. *Distal oral shield* indistinct. *Frontal shield* tapered proximally. *Costae* very numerous, 18–22, closely placed. Number of *pelmata* and *lateral costal fusions* not determinable. *Apertural bar* apparently fairly wide, straight, with at least two large pelmata, one at each end. *Gymnocyst* exposed proximally to the frontal shield, apparently not obscured by *interzooecial secondary tissue.*

Avicularia apparently of one kind only, a prominent, large, lateral oral pair. It cannot be determined, from the photograph, whether or not the lateral oral avicularia unite above the orifice to produce a complete proximal oral shield. *Ovicells* not seen.

MEASUREMENTS. [According to Lang, 1922 : 376.]
Zooecia Lz = About 1·10 mm.
lz = About 0·49 mm.

REMARKS. On the evidence obtainable from the photograph of the specimen (in Mons. F. Canu's Collection) Lang placed it as a species of *Batrachopora* [=*Ubaghsia*.]. This is apparently correct, judging from the general form of the secondary orifice and its proximal shield. The figure given by Lang (1922 : 375, text-fig. 119) is, however, largely hypothetical. The photograph is not sufficiently clear to show the precise shape of the oral avicularia, and certainly not clear enough to allow any accurate assessment of the number of pelmata or lateral costal fusions.

If the specimen is correctly placed as a species of *Ubaghsia* it is clearly distinguishable from other species of the genus by its unusually high number of costae, 18–22, and its single kind of avicularia.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian.

SPECIMEN. Only a photograph of the holotype in the F. Canu Collection. Royan, south of Rochefort, Charente-Inférieure, France.

3. *Ubaghsia gasteri*[1] sp. nov.

(Pl. 20, figs. 4, 7 ; Text-figs. 118–120)

HOLOTYPE. D.40546. Unattached zoarial fragment. Senonian, lower part of zone of *G.* [*A.*] *quadrata*. Pit 21 of Gaster, northernmost of two pits on Patching Hill, Patching, Sussex.

PARATYPES. D.40547. Unattached zoarial fragment. Horizon, locality and collection as for the holotype.

D.40548. Unattached zoarial fragment. Senonian, lower part of zone of *G.* [*A.*] *quadrata*. Pit 15*a* of Gaster, small pit by roadside, south-east of Salvington Windmill, north-west of large pit (No. 15 of Gaster), and south of Pit 14 of Gaster, Salvington, Sussex.

DIAGNOSIS. *Ubaghsia* with closely placed zooecia (Lz = 0·80 to 0·93 mm., lz = 0·50 to 0·63 mm.) ; secondary orifice relatively large (hr = 0·19 to 0·25 mm., lr = 0·20 to 0·25 mm.), of variable shape, usually a little wider than high or of equal height and width, but occasionally a little higher than wide, smaller than the frontal shield ; distal oral shield present, proximal oral shield prominent ; oral spines 4 ; frontal shield flat, not descending steeply to meet the gymnocyst ; costae 9 or 10 (very occasionally more), each with two lateral costal fusions and pelmata ; interzooecial secondary tissue abundant ; avicularia of two kinds : (*a*) a large, prominent, proximal-lateral oral pair, (*b*) an occasional small, rounded, interzooecial form.

DESCRIPTION. *Zoarium* probably encrusting (but all specimens fragmentary and now unattached), unilaminar. *Zooecia* broadly oval, closely placed. *Secondary orifice* large, but much smaller than the frontal shield, usually a little wider than high, or of equal height and width, but occasionally slightly higher than wide. The shape of the orifice varies from almost square to rounded distally, with straight sides and a straight proximal margin. Proximal-lateral constrictions are visible in some orifices, particularly those with worn rims. *Distal oral shield* formed by the distal oral spines and secondary tissue ; *proximal oral shield* very prominent, formed mainly by the proximal-lateral oral avicularia with the distal-lateral pair of oral spines apparently fused on to the distal sides of the avicularia. *Oral spines* 4, enlarged, thickened, partly embedded in secondary tissue, hollow and cylindrical, arranged as a distal and a distal-lateral pair—the latter may be fused on to the distal sides of the lateral oral avicularia. *Frontal shield* flat : the edges may be partly

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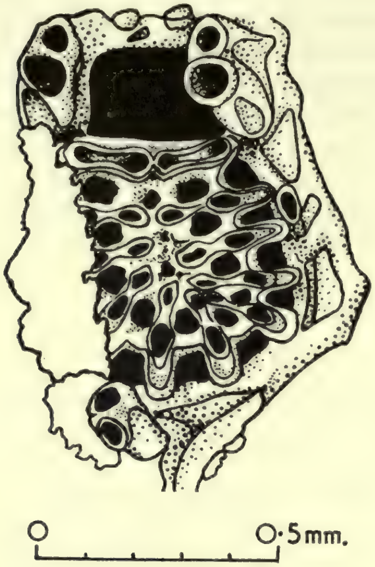
[1] After C. T. A. Gaster.



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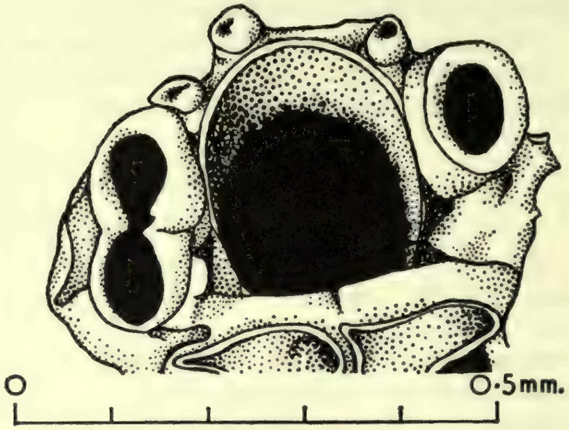

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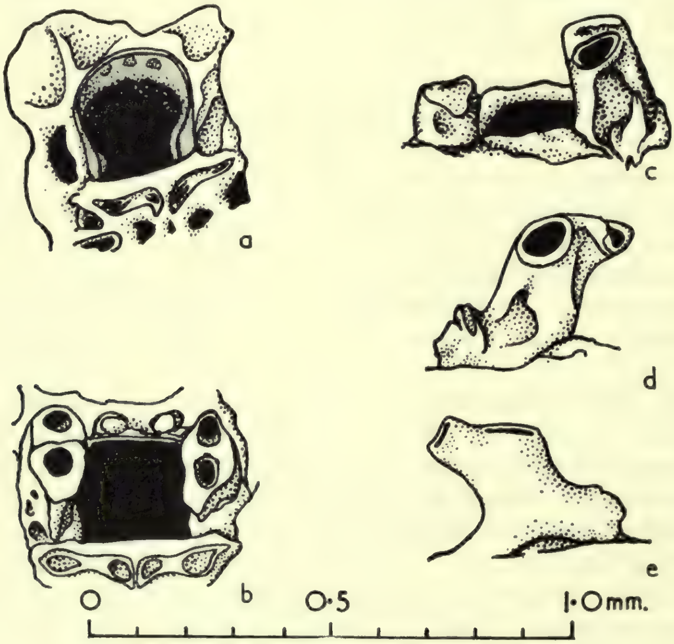

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FIGS. 118–120. *Ubaghsia gasteri* sp. nov.

(118) D.40548. Paratype. Adult zooecium with worn, but very prominent, proximal-lateral oral avicularia fused to distal-lateral pair of oral spines. A small oval avicularium of type *b* occurs near the right edge of the frontal shield.

(119) D. 40546. Holotype. (*a*) Worn orifice of adult zooecium with proximal-lateral constrictions in the primary orifice. (*b*) Orifice of adult zooecium showing the square form produced by proximal oral shield. (*c*, *d*, *e*) Proximal, inner and outer views respectively of one side of a broken proximal oral shield showing the proximal-lateral oral avicularia fused with the distal-lateral oral spines.

(120) D.40546. Holotype. Orifice of adult zooecium with worn proximal-lateral oral avicularia and worn oral spines.

concealed by expansions of the interzooecial secondary tissue. *Costae* 9 or 10, very occasionally 13, tapering inwards, wide at their outer ends, where they descend slightly to meet the gymnocyst. Each costa carries a large, prominently rimmed *pelma* near its outer end and one, occasionally two, other pelmata nearer to the inner end. *Lateral costal fusions* arise at the levels of the pelmata, producing irregular intercostal spaces. *Apertural bar* straight, thickened, particularly at each end, and bearing two large pelmata and a pair of smaller pelmata between them nearer to the mid-line, which may be slightly furrowed. *Gymnocyst* almost entirely concealed by the close placing of the zooecia, which may result in the frontal shields of adjacent zooecia appearing contiguous, and by abundant *interzooecial secondary tissue* which generally fills the interzooecial valleys and in places expands on to the frontal shields. The interzooecial secondary tissue is marked by slight, irregular ridges surrounding shallow *lacunae.*

Avicularia of two kinds : (*a*) a very prominent proximal-lateral form, well raised on stout stalks with secondarily thickened walls, paired, one on each side of, and very close to, the orifice, (*b*) an occasional, interzooecial form which is very small, and distally pointed and directed. Avicularia of type (*a*) probably did not unite above the secondary orifice to form a complete proximal oral shield. Each of the lateral oral avicularia may be fused on its distal side to one of the distal-lateral pair of oral spines. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 0·80 to 0·93 mm.
lz = 0·50 to 0·63 mm.
hr = 0·19 to 0·25 mm.
lr = 0·20 to 0·25 mm.
Avicularia Not measurable.

REMARKS. *U. gasteri* is distinguished from other species of *Ubaghsia* by the close placing of its zooecia, the four thickened, often visibly separate, oral spines and the form of the frontal shield which does not descend steeply at the edges. The zoarial fragments were probably encrusting, but the specimens are broken and no longer attached. Two worn avicularia of type (*b*) are present in D.40548.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *G.* [*A.*] *quadrata.*

SPECIMENS. D.40546, holotype and D.40547–48, two paratypes—see above.

4. ***Ubaghsia langi***[1] sp. nov.

(Pl. 21, figs. 4, 5 ; Text-figs. 121–123)

HOLOTYPE. N.C.M.247.956 (4/1). Incomplete zoarium encrusting a test of *Conulus albogalerus.* Senonian, zone of M. *cor-anguinum.* Northfleet, Kent. A. W. Rowe Collection.

DIAGNOSIS. *Ubaghsia* with closely placed zooecia (Lz = 0·73 to 0·80 mm., lz = 0·50 to 0·60 mm.) ; secondary orifice fairly large, wider than high or of equal height and width, smaller than the frontal shield ; oral spines 4, much thickened and enlarged ; frontal shield flat, very steeply descending at the outer edges ; costae

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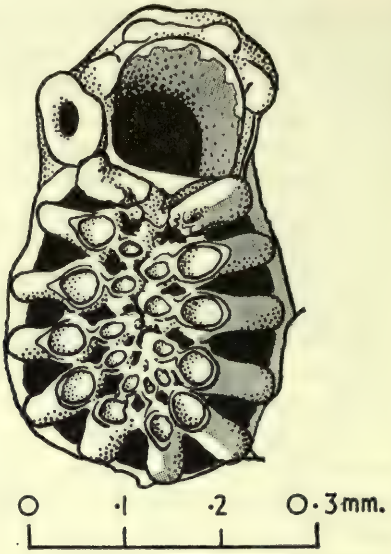
[1] After W. D. Lang.



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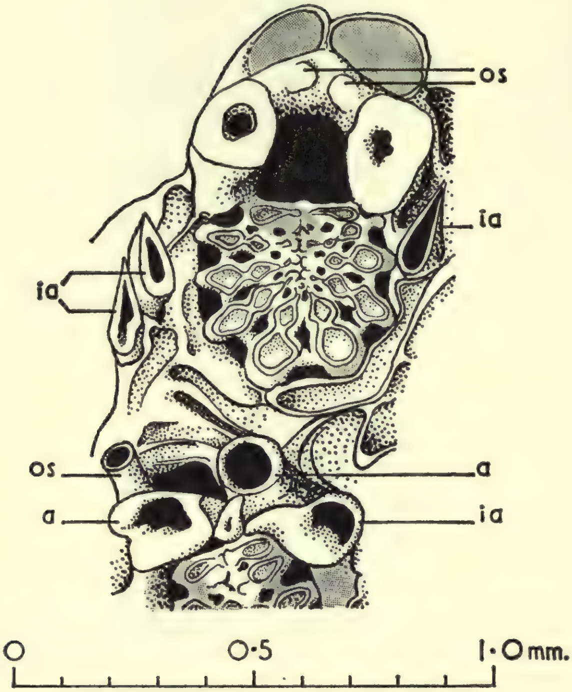

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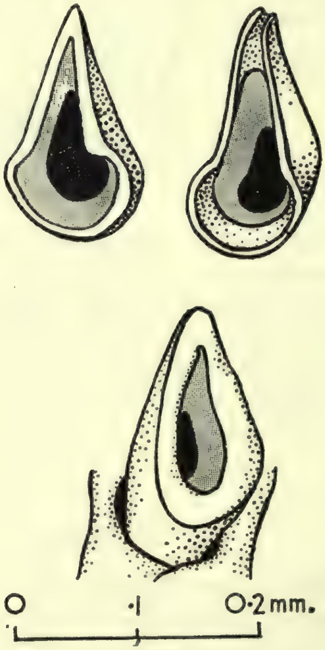

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Figs. 121–123. *Ubaghsia langi* sp. nov. N.C.M.247.956 (4/1).

(121) Holotype. Adult zooecium and part of a proximally adjacent zooecium: ***a***, proximal-lateral oral avicularia forming proximal oral shield; *ia*, interzooecial avicularia; *os*, distal oral spines.

(122) Young zooecium; the rim of the secondary orifice is damaged.

(123) Three interzooecial avicularia.

7–10; lateral costal fusions 2 or 3; avicularia of two kinds: (*a*) a prominent, large, proximal-lateral oral pair, very close to the orifice, raised on stout stalks and united above the orifice to produce a strong proximal shield, (*b*) a prominent, frequent, distally pointed and directed, interzooecial form.

DESCRIPTION. *Zoarium* unilaminar, encrusting. *Adult zooecia* broadly oval, closely spaced. *Secondary orifice* wider than high, its form obscured by the proximal and distal oral shields. The rim of the secondary orifice is much thickened by secondary tissue which incorporates the much enlarged oral spines. The orifice is rounded distally with straight sides and a straight proximal margin. *Oral spines* in two pairs, much enlarged and thickened. *Distal oral shield* formed by the pair of distal oral spines and secondary tissue. *Proximal oral shield* very prominent, produced by the upgrowth and median fusion above the orifice of the very large lateral oral avicularia, often fused with the distal-lateral pair of oral spines. Occasionally the proximal shield may be enlarged by the additional incorporation of an enlarged interzooecial avicularium (*ia.* in Text-fig. 121). *Frontal shield* flat within the outermost lateral costal fusions, but outwards from them the costae descend very steeply to meet the obscured gymnocyst. *Costae* 7–10, stout, each with a very prominent *pelma* nearer the outer end, and, towards the inner end, one, or often two, smaller *pelmata*. *Lateral costal fusions* arise at the levels of the pelmata producing very irregular *intercostal spaces* in the wide median area. *Apertural bar* prominent, straight, with a pelma near each of the outer ends and another pelma near the mid-line. *Gymnocyst* obscured by fairly abundant *interzooecial secondary tissue* which almost fills the interzooecial valleys and contains irregular shallow *lacunae*. The secondary tissue forms a *tertiary front wall* which connects the proximal and distal oral shields of the zooecia, and often encroaches on to the edges of the frontal shields or stands up above their general level as a ridge.

Avicularia of two kinds: (*a*) a very large, thickened, heavily calcified lateral oral pair, raised on stout stalks, very close to, and one on either side of, the orifice. These unite above the orifice to produce the very prominent proximal oral shield; (*b*) an interzooecial form, fairly prominent, frequent, unpaired, distally pointed and directed, lacking a transverse bar, but laterally constricted, producing a semicircular proximal portion and a triangular *rostrum*. Secondary thickening of avicularia of type (*b*) is variable. *Ovicells* not seen.

Young zooecia small. *Orifice* of equal height and width. *Oral spines* 4, thickened, the distal pair not so enlarged as the distal-lateral pair. *Frontal shield* very well arched but flat on top. *Costae* 9 or 10, not so closely placed as in the adult zooecia, each with a very large, prominent, *pelma*, and, inwards from this, one, occasionally two, *pelmatidia*. The pelmata form a conspicuous ring round the flat median area. Outwards from them the costae descend very steeply to meet the gymnocyst. *Lateral costal fusions* occur at the levels of the pelmata and pelmatidia, producing very irregular *intercostal spaces*. *Apertural bar* thickened, prominent, relatively straight, with two pelmata near the mid-line. *Gymnocyst* smooth; widely exposed, especially proximally to the frontal shield. There is some *interzooecial secondary tissue* but this does not fill, or extend from, the interzooecial valleys as in the adult stages. *Avicularia* of two kinds: (*a*) a lateral oral pair, raised on stout stalks, and apparently not uniting to form a complete proximal oral shield ; (*b*) an occasional, sporadic, unpaired, rounded, small, interzooecial form.

MEASUREMENTS. *Adult zooecia* Lz = 0·73 to 0·80 mm.
lz = 0·50 to 0·60 mm.
hr = 0·20 mm.
lr = 0·20 to 0·23 mm.
Avicularia of type (*a*) Lz = 0·20 mm.
lz = 0·11 mm.
Young zooecia Lz = 0·53 to 0·62 mm.
lz = 0·30 to 0·32 mm.
hr = 0·12 mm.
lr = 0·12 mm.

REMARKS. *Ubaghsia langi* is distinguished from *U. gasteri* particularly by its more numerous, larger, distally pointed, interzooecial avicularia, and by its smaller size and generally fewer costae. The holotype encrusts a test of *Conulus albogalerus* from the Senonian, zone of *M. cor-anguinum*. On the base of the same echinoid is a well-preserved zoarial fragment of *Lagynopora horsleyensis* Lang, N.C.M.247.956 (4/2), a species recorded previously from the higher *M. cor-anguinum* Chalk. *Ubaghsia langi* is, as yet, the earliest known *Ubaghsia*. It does not have the features which Lang (1922 : 395) regarded as " primitive " for the genus, i.e., a large number of costae and a small size compared with the Maastrichtian species.

STRATIGRAPHICAL DISTRIBUTION. Senonian, higher part of zone of *M. cor-anguinum*.

MATERIAL. N.C.M.247.956 (4/1). Holotype—see above.

5. *Ubaghsia crassa* (Lang)

(Pl. 20, fig. 5 ; Pl. 21, fig. 7 ; Text-fig. 124)

1916*a* *Batrachopora crassa* Lang, pp. 110, 111.
1919*d* *Batrachopora crassa* Lang : Lang, pp. 206, 208, 217, 219, 221, text-fig. 83.
1922 *Batrachopora crassa* Lang : Lang, p. 365, pl. 8, fig. 3 ; text-fig. 116.
1925*b* *Batrachopora crassa* Lang : Voigt, p. 104.
1930 *Batrachopora crassa* Lang : Voigt, p. 551.

HOLOTYPE. D.16674. Poorly preserved zoarial fragment encrusting a cheilostome polyzoan ; only one worn zooecium is complete, in all others the frontal shield is destroyed. Labelled by Lang " *Batrachopora crassa*. Senonian, zone of *B. mucronata*, Rügen "—probably Maastrichtian. Agnes Laur Collection.

EMENDED DIAGNOSIS. *Ubaghsia* with fairly closely placed large zooecia (Lz = 1·00 to 1·12 mm., lz = 0·66 to 0·82 mm.) ; secondary orifice relatively large, wider than high (hr = 0·22 to 0·26 mm., lr = 0·28 to 0·30 mm.), smaller than the frontal shield ; oral spines at least 4 ; frontal shield flat, descending at the outer edges ; costae 7, each with 2 (very occasionally 3) lateral costal fusions and pelmata ; interzooecial secondary tissue fairly abundant ; avicularia of two kinds : (*a*) a large lateral oral pair, (*b*) an occasional, small, sporadic, interzooecial form.

Description. *Zoarium* encrusting, unilaminar. *Zooecia* broadly oval, less closely placed than in *U. gasteri*. *Secondary orifice* large, but smaller than the frontal shield, wider than high, shape variable from square or oblong to rounded distally with straight sides and a straight proximal margin. *Oral spines* probably at least 4, thickened but not lengthened, a distal pair visible in the rim of secondary tissue and a distal-lateral pair apparently fused on to the distal sides of the lateral oral avicularia. *Distal oral shield* indistinct. *Proximal oral shield* formed by the distal-lateral oral spines fused with the lateral oral avicularia which probably united above the orifice. *Frontal shield* occasionally somewhat arched, but commonly flat over most of its width, descending steeply at the outer edges. *Costae* of unusually constant number, 7, each with 2 (very occasionally 3) stout *lateral costal fusions* arising at the levels of large, prominent *pelmata*. A distinct ridge surrounds the pelmata and is apparently continuous on the upper surface of each costa between the pelmata. *Pelmatidia* may occur irregularly very close to the mid-line. *Apertural bar* broad, straight, with the outer ends bent distally, widening near the mid-line, with a straight median furrow and bearing two very large, elongate pelmata. *Gymnocyst* smooth, partly concealed by fairly abundant, irregularly

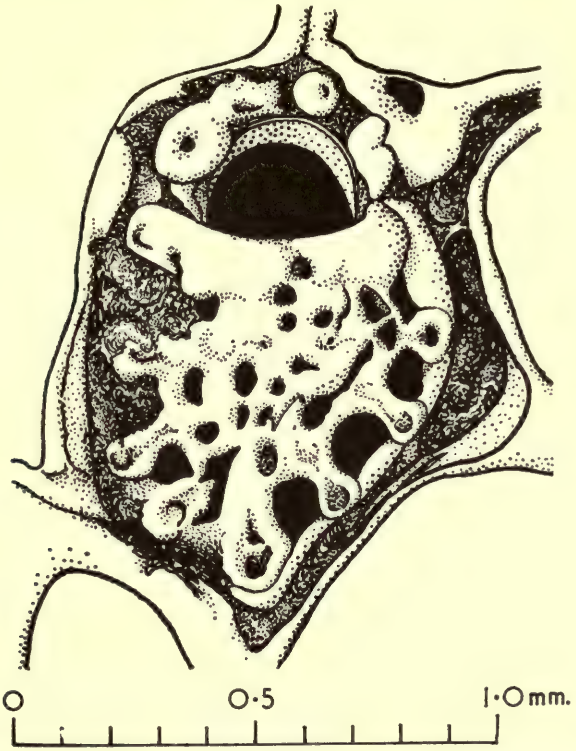


Fig. 124. *Ubaghsia crassa* (Lang), D. 16674. Holotype. Very worn adult zooecium—the only complete zooecium in the holotype zoarial fragment.

distributed *interzooecial secondary tissue*, which may in places expand on to the edges of the frontal shields. Irregular, shallow *lacunae* occur in the interzooecial tissue.

Avicularia of two kinds : (*a*) a very prominent, large lateral oral pair, well raised on stout stalks, with secondarily thickened walls, occurring very close to, and one on either side of, the orifice ; (*b*) an occasional, small, sporadic, interzooecial form. Avicularia of type (*a*) probably united above the orifice to produce a complete proximal oral shield. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 1·00 to 1·12 mm.
lz = 0·66 to 0·82 mm.
hr = 0·22 to 0·26 mm.
lr = 0·28 to 0·30 mm.
Avicularia Not measurable.

REMARKS. Lang (1922 : 368) based his description of *Batrachopora crassa* on the holotype, D.16674, the only specimen available. Unfortunately, it is badly damaged and worn, the details of the pelmata, oral spines and avicularia being particularly uncertain. The dimensions of its only complete zooecium are : Lz = 1·10 mm., lz = 0·75 mm., hr = 0·22 mm., lr = 0·30 mm. There are 7 costae, each with at least two pelmata and lateral costal fusions. These characters compare very closely with those found in N.C.M.76.937 (30), which is a better preserved zoarial fragment encrusting a piece of echinoid test.

He suggested that interzooecial secondary tissue is scanty and the gymnocyst widely exposed. This opinion was based on the very worn holotype where most of the frontal shields and much of the interzooecial tissue have been destroyed. N.C.M.76.937 (30), however, has fairly plentiful interzooecial secondary tissue. Avicularia are of two kinds, the oral pair being large and prominent, not, as Lang has stated, " apparently confined to a comparatively small, somewhat raised, apertural [oral] pair ".

N.C.M.76.937 (30) from the *B. mucronata* Chalk of Catton, Norfolk, extends the downward range of *Ubaghsia crassa* from the Rügen horizon.

STRATIGRAPHICAL DISTRIBUTION. Probably Maastrichtian, and Senonian, zone of *B. mucronata*.

SPECIMEN. D.16674. Holotype—see above.

OTHER MATERIAL. N.C.M.76.937 (30). Zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Catton, near Norwich, Norfolk. R. M. Brydone Collection.

6. *Ubaghsia coaxans* (Lang)

(Pl. 20, fig. 6 ; Pl. 21, fig. 6 ; Text-fig. 125)

1916*a* *Batrachopora coaxans* Lang, p. 111.
1919*d* *Batrachopora coaxans* Lang : Lang, pp. 206, 208, 221, text-fig. 84.
1922 *Batrachopora coaxans* Lang : Lang, p. 377, pl. 8, fig. 5 ; text-fig. 120.
1930 *Batrachopora coaxans* Lang : Voigt, p. 551.

Holotype. D.14209. Fragment of zoarium, now unattached, with two complete zooecia. Labelled by Lang " *Batrachopora coaxans*. Upper Senonian, Rügen " —probably Maastrichtian. Agnes Laur Collection.

Emended diagnosis. *Ubaghsia* with zooecia 1·07 to 1·15 mm. long, 0·78 to 0·83 mm. wide, secondary orifice wider than high (hr = 0·25 to 0·26 mm., lr = 0·31 to 0·35 mm.) ; costae 11–14, each with 3 or 4 lateral costal fusions and pelmata ; avicularia apparently of two kinds : (*a*) a large lateral oral pair, (*b*) a somewhat smaller, occasional, unpaired interzooecial form.

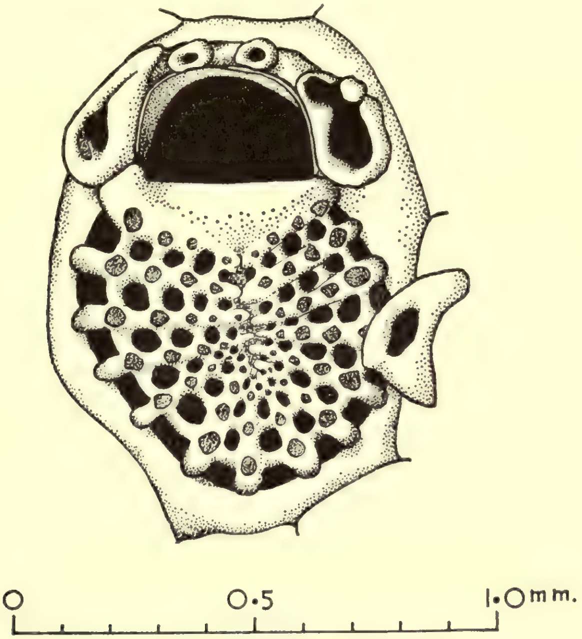


Fig. 125. *Ubaghsia coaxans* (Lang), D. 14209. Holotype. Adult zooecium with broken proximal oral shield.

Description. *Zoarium* unilaminar, now unattached but probably encrusting. *Zooecia* very broadly oval. *Secondary orifice* wider than high, much smaller than the frontal shield, rounded distally, sides and proximal margin straight. *Distal oral shield* indistinct. *Proximal oral shield* formed by the paired, large lateral oral avicularia which possibly united above the orifice. *Oral spines* probably at least 4 ; a distal pair of thickened and slightly enlarged, but not markedly lengthened, oral spines is almost completely immersed in the secondary tissue of the rim of the orifice, and a distal lateral pair probably fused on to the distal sides of the lateral oral avicularia, thus forming part of the proximal oral shield. *Frontal shield* wide, flat except at the margins. *Costae* 11–14, narrow. Near the outer end of each costa is a relatively small *pelma*, outwards from this each costa slopes down more steeply to meet the gymnocyst ; inwards from this pelma each costa is level and carries another two, more commonly three, *smaller pelmata*. *Lateral costal fusions* 3 or 4 (corresponding in number to the pelmata), narrow, those at the level of the outermost pelmata arcuate. *Intercostal spaces* regularly arranged. *Apertural bar* wide, flat, straight, with 3 or 4 small pelmata. *Gymnocyst* smooth, well exposed, particularly proximally to the frontal shield, not obscured by *interzooecial secondary tissue* which is absent or only slightly developed.

Avicularia apparently of two kinds : (*a*) a large, prominent, lateral, oral pair with much thickened walls, (*b*) a somewhat smaller, occasional, unpaired, sporadic, rounded interzooecial form. Avicularia of type (*a*) were raised to some extent on thickened, stout stalks, and possibly fused above the orifice, but in the available material they are all worn down to the level of the secondary orifice. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 1·07 to 1·15 mm.
lz = 0·78 to 0·83 mm.
hr = 0·25 to 0·26 mm.
lr = 0·31 to 0·35 mm.

REMARKS. *Ubaghsia coaxans* is clearly distinguished by its numerous costae, pelmata and lateral costal fusions, and its dimensions. It is not possible to decide, on the available evidence, whether or not the oral avicularia united above the orifice.

STRATIGRAPHICAL DISTRIBUTION. Specimens labelled " Upper Senonian, Rügen ", but probably boreal Maastrichtian.

SPECIMENS. D.14209. Holotype—see above.

D.15041. Paratype. Zoarial fragment, now unattached. Labelled by Lang " *Batrachopora coaxans* ". Horizon, locality and collection as for the holotype.

7. ***Ubaghsia perforata*** (Marsson)

1887	*Cribrilina perforata* Marsson, pp. 98, 109, pl. 10, fig. 11.
1895	*Cribillina* [*sic*] *perforata* Marsson : Deecke, p. 80.
1900*b*	*Cribrilina perforata* Marsson : Canu, p. 445.
1916*a*	*Batrachopora perforata* (Marsson) Lang, pp. 110, 111.
1919*d*	*Batrachopora perforata* (Marsson) : Lang, pp. 206, 219, 221.
1921	*Batrachopora perforata* (Marsson) : Lang, p. xci.
1922	*Batrachopora perforata* (Marsson) : Lang, p. 362.
1925	*Cribrilina brachiata* Levinsen, p. 377, pl. 8, fig. 24.
1927	*Cribrilina brachiata* Levinsen : Voigt, p. 102.
1930	*non Stichocados ordinatus* Lang : Voigt, p. 510, pl. 30, fig. 14.

LECTOTYPE. (Chosen by Lang, 1922 : 362.) The specimen figured by Marsson, 1887, pl. 10, fig. 11. " Schreibkreide of Rügen " (? boreal Maastrichtian).

EMENDED DIAGNOSIS. *Ubaghsia* with encrusting or unattached zoarium ; secondary orifice wider than high, much smaller than the frontal shield ; costae 10–13, each with at least 3 lateral costal fusions ; avicularia apparently of two kinds : (*a*) a prominent lateral oral pair (*b*) ? occasional interzooecial forms ; [length of zooecia given by Lang (1922 : 362) as about 0·73 mm.].

REMARKS. Although Levinsen (1925 : 377, pl. 8, fig. 24) introduced *Cribrilina brachiata* as a new species, he himself suggested by its synonymy that it might be the same as *C. perforata* Marsson. I accept their synonymy, and although Levinsen's figure is obscure, the diagnosis of *Ubaghsia perforata* may be expanded as above to include Levinsen's species. I do not accept Voigt's (1930 : 510) placing of the species as synonymous with *Stichocados ordinatus* Lang. Levinsen's specimen was encrusting; Marsson's material was unattached. Lang (1922 : 362) regarded the species as " primitive in most of its features ".

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian, possibly extending downwards into the Senonian, upper part of the zone of *B. mucronata*.

SPECIMENS. None in the collection.

8. ***Ubaghsia ocellata*** (Jullien)

(Pl. 22, figs. 1, 2)

1886 *Steginopora ocellata* Jullien, p. 614, pl. 19, figs. 1–3.
1900*b* *Steginopora ocellata* Jullien : Canu, pp. 453, 454, text-fig. 66 [a reduced copy of Jullien, 1886, pl. 19, figs. 1–3].
1916*a* *Ubaghsia ocellata* (Jullien) Lang, p. 99.
1920 *Steginopora ocellata* Jullien : Canu & Bassler, p. 282, text-fig. 81S [a reduced copy of Jullien, 1886, pl. 19, fig. 1].
1921 *Ubaghsia ocellata* (Jullien) : Lang, p. xciii.
1922 *Ubaghsia ocellata* (Jullien) : Lang, p. 226.
1929 *Steginopora ocellata* Jullien : Canu & Bassler, p. 243.

LECTOTYPE. (Chosen by Lang, 1922 : 226.) The specimen figured by Jullien, 1886, pl. 19, fig. 1. " Etage sénonien. Port Brehay ", north-east of Gourbesville, north-west of Carentan, Manche, France. [Horizon probably middle or lower parts of zone of *B. mucronata*.]

EMENDED DIAGNOSIS. (Based on Jullien's figures and description of the species.) *Ubaghsia* with unilaminar, apparently unattached zoarium; distal oral spines bifurcate; orifice large, transversely elongate, almost oblong to rounded oblong, with straight proximal margin, much smaller than the convex frontal shield; number of costae, lateral costal fusions, and pelmata uncertain; avicularia of two kinds: (*a*) a large prominent, well-raised, lateral oral pair, (*b*) a single, occasionally paired, small, vicarious form, directed variously but always outwards from the zooecium it accompanies, distally pointed and divided by a straight transverse bar into a triangular rostrum and a smaller semicircular proximal portion; tertiary front wall complete, with a median depression containing two or three lacunae, and two or three more lacunae symmetrically placed near the margin: other lacunae, of about the size of the orifice, occur interzooecially.

REMARKS. Lang (1922 : 226) stated " having simpler apertural [oral] spines than *Ubaghsia demorgani* and *M.* [*sic*] *meudonensis*, *M.* [*sic*] *ocellata* is probably more primitive than these; its relationship to *M.* [*sic*] *reticulata* is doubtful ". However, *Ubaghsia ocellata* may be readily distinguished from *U. reticulata*, which has unbranched distal oral spines and a very irregular tertiary front wall. *U. meudonensis* and *U. demorgani* have more complex oral spines, each being branched from three to six times ; this feature particularly distinguishes these two species from *U. ocellata*. The tertiary front walls of the latter and of *U. demorgani* are, however, very similar.

STRATIGRAPHICAL DISTRIBUTION. Senonian, ? lower or middle part of zone of *B. mucronata*.

SPECIMENS. None in the collection.

9. *Ubaghsia meudonensis* (Jullien)

(Pl. 22, figs. 3, 4)

1886 *Steginopora meudonensis* Jullien, p. 614, pl. 17, figs. 1–5 ; pl. 18, figs. 1–3.
1916*a* *Ubaghsia meudonensis* (Jullien) Lang, pp. 99, 100.
1921 *Ubaghsia meudonensis* (Jullien) : Lang, p. xci.
1922 *Ubaghsia meudonensis* (Jullien) : Lang, p. 228.

LECTOTYPE. (Chosen by Lang, 1922 : 228). The specimen figured by Jullien, 1886, pl. 17, fig. 3. " Etage sénonien." Les Moulineaux, near Meudon, south-west of Paris. Zone of *B. mucronata*.

EMENDED DIAGNOSIS. (Based on Jullien's figures and description of the species.) *Ubaghsia* with unilaminar, encrusting zoarium ; distal oral spines with from two to six branches ; orifice large, as wide as high, rounded distally, sides and proximal margin straight, smaller than the frontal shield ; number of costae, lateral costal fusions and pelmata unknown ; avicularia of two kinds : (*a*) a large, prominent, well-raised, lateral oral pair, (*b*) a smaller, interzooecial form, usually paired but occasionally single or absent, often raised on a stout stalk, variously directed, with a small, lunate, proximal portion divided by a curved transverse bar from a triangular rostrum ; tertiary front wall apparently much thicker than in *U. ocellata* and *U. demorgani*, containing irregular large and small lacunae and well-marked secondary orifices.

REMARKS. *U. meudonensis* possesses a more robust tertiary front wall than *U. demorgani*, but differences in this character alone may be insufficient to keep the two species distinct. However, until specimens are available for study these two species are maintained as separate.

See also remarks on *U. ocellata*, (p. 255).

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *B. mucronata*.

SPECIMENS. None in the collection.

10. *Ubaghsia demorgani* (Jullien)

(Pl. 22, figs. 5, 6)

1886 *Steginopora demorgani* Jullien, p. 615, pl. 19, figs. 4, 5 ; pl. 20, fig. 1.
1916*a* *Ubaghsia demorgani* (Jullien) Lang, p. 99, 100.
1921 *Ubaghsia demorgani* (Jullien) : Lang, p. xci.
1922 *Ubaghsia demorgani* (Jullien) : Lang, p. 227.

LECTOTYPE. (Chosen by Lang, 1922 : 227.) The specimen figured by Jullien, 1886, pl. 19, fig. 4. " Etage sénonien, craie de Meudon (Les Moulineaux)." Meudon, south-west of Paris. Zone of *B. mucronata*.

EMENDED DIAGNOSIS. (Based on Jullien's figures and description of the species.) *Ubaghsia* with bilaminar zoarium; distal oral spines with three or four branches; orifice large, transversely elongate-oval or almost oblong, or rounded distally with straight sides and a straight proximal margin, much smaller than the convex frontal shield; number of costae, lateral costal fusions, and pelmata not known; avicularia of two kinds: (*a*) a large, prominent, well-raised, lateral oral pair, (*b*) a small, vicarious form, commonly paired but occasionally single or absent, directed variously, but always outwards from the zooecium it accompanies, distally pointed and divided by a straight transverse bar into a triangular rostrum and a smaller, semicircular proximal portion; tertiary front wall complete, with the orifice markedly transversely elongate, and the lacunae and median depression similar to those of *U. ocellata* in number and arrangement, though the interzooecial lacunae are apparently much smaller than those of that species.

REMARKS. See remarks on *U. ocellata* (p. 255) and *U. meudonensis*, p. 256).

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *B. mucronata.*

SPECIMENS. None in the collection.

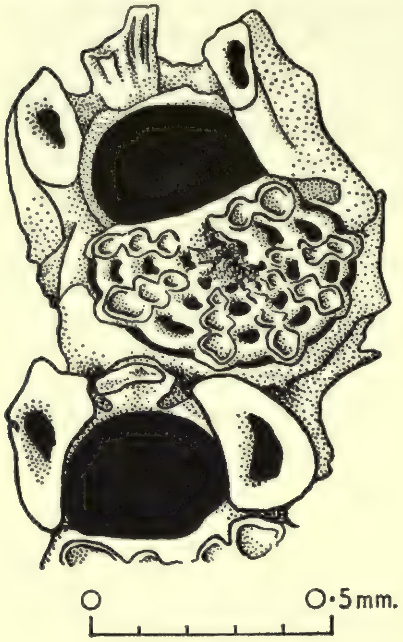
11. *Ubaghsia reticulata* (Ubaghs)

(Pl. 21, figs. 1–3; Pl. 22, figs. 7, 8; Text-figs. 126–128)

1865 *Steginopora reticulata* Ubaghs, p. 55, pl. 2*a*, fig. 7*a–d*.
1886 *Ubaghsia reticulata* (Ubaghs) Jullien, pp. 610, 612, 616, pl. 18, figs. 4, 5.
1916*a* *Ubaghsia reticulata* (Ubaghs): Lang, p. 99.
1916*a* *Batrachopora hyla* Lang, pp. 111, 112.
1919*d* *Batrachopora hyla* Lang: Lang, pp. 205, 208, 219, 221, text-fig. 82.
1921 *Ubaghsia reticulata* (Ubaghs): Lang, pp. lxvi, xc.
1921 *Batrachopora hyla* Lang: Lang, p. xc.
1922 *Ubaghsia reticulata* (Ubaghs): Lang, p. 227.
1922 *Batrachopora hyla* Lang: Lang, p. 364, pl. 8, fig. 2; text-fig. 115.
1922 *Batrachopora ornata* (Goldfuss): Lang, p. 370 [*partim*—pl. 8, fig. 4, specimen D.1391 only].
1929 *Steginopora reticulata* Ubaghs: Canu & Bassler, p. 244.
1930 *Ubaghsia reticulata* (Ubaghs): Voigt, p. 513 [*partim*], pl. 31, fig. 19 only, *non* fig. 20.
1930 *Batrachopora ornata* (Goldfuss): Voigt, p. 515, pl. 31, fig. 18.
1930 *Batrachopora hyla* Lang: Voigt, p. 515.
1935 *Steginopora reticulata* Ubaghs: Bassler, p. 222.
1953 *Steginopora reticulata* Ubaghs: Bassler, p. G193.
1953 *Ubaghsia reticulata* (Ubaghs): Bassler, p. G193, text-fig. 144, 30.

LECTOTYPE. (Chosen by Lang, 1922: 227.) The specimen figured by Ubaghs, 1865, pl. 2*a*, fig. 7*c*. Maastrichtian. Ober Bryozoenschichte (horizon *f* of Ubaghs). Valkenburg (Fauquement), east of Maastricht, or Geulem, north-east of Maastricht, Holland.

EMENDED DIAGNOSIS. *Ubaghsia* with unbranched distal oral spines; zooecia 0·80 to 0·85 mm. long 0·60 to 0·72 mm. wide; secondary orifice wider than high (hr = 0·20 to 0·25 mm., lr = 0·26 to 0·35 mm.); costae 4–7 (often 5 or 6) each with 3 (occasionally 2) lateral costal fusions and pelmata; avicularia of two kinds: (*a*) a large lateral oral pair, (*b*) small, rounded, occasionally paired, interzooecial forms.



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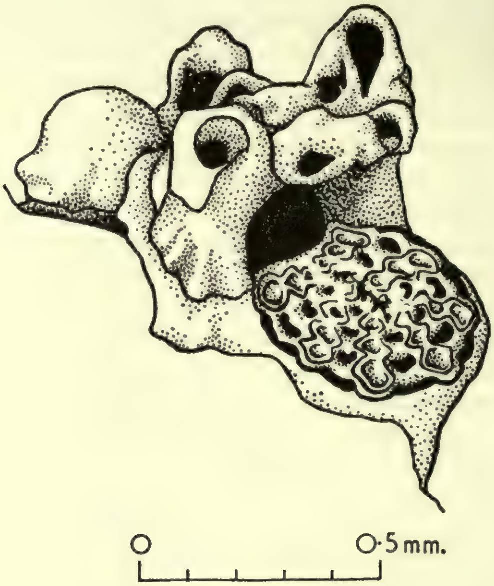

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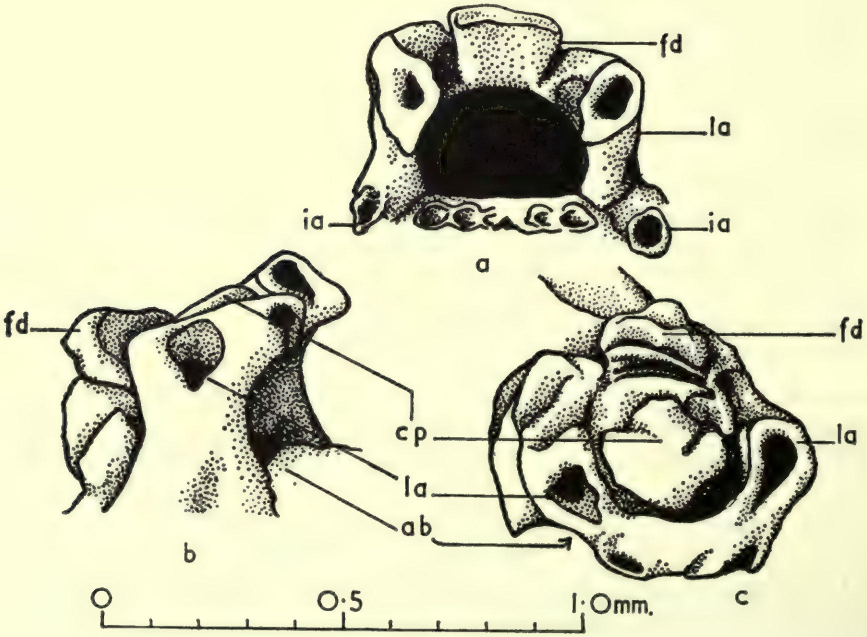
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DESCRIPTION. *Zoarium* unilaminar, probably encrusting. *Zooecia* broadly oval, smaller than in *U. ornata*. *Secondary orifice* very large, wider than high, almost as large as the frontal shield, rounded distally and laterally with a straight proximal margin. The orifice is surrounded by complete distal and proximal oral shields. The *distal oral shield* is formed by the amalgamation of the pair of distal oral spines which are enlarged and joined by secondary tissue. The *proximal oral shield* is composed of the very large, paired oral avicularia, which fuse above the apertural bar and orifice, and which incorporate on their distal sides the distal-lateral oral spines. *Oral spines* originally 4, rapidly enlarged but unbranched, united by secondary tissue to form parts of the distal and proximal oral shields. *Frontal shield* generally flat, broadly oval. *Costae* 4–7 (often 5–6), broad, irregular, tapering inwards ; near the outer end of each costa is a large *pelma*, outwards from which the ends of the costae bend down abruptly to meet the gymnocyst, while inwards there is one other *pelma* of large size and commonly, nearer the mid-line a third *pelma*. No other definite pelmata or pelmatidia have been seen. *Lateral costal fusions* occur opposite the pelmata, so that there are normally at least three pairs on each costa producing irregular, somewhat lacunate, *intercostal spaces*. *Apertural bar* not prominently thickened, straight, with at least two, often three, pairs of pelmata. *Gymnocyst* smooth, particularly exposed proximally to some frontal shields.

Avicularia of two kinds : (*a*) a very large lateral oral pair raised on much thickened stalks, one on either side, of, and close to, the lateral margins of the orifice, (*b*) a small, rounded, interzooecial form which is apparently sometimes paired, one near each end of the apertural bar and a little proximal to it. Avicularia of type (*a*) make up an essential part of the proximal oral shield ; the unmodified form of these avicularia has not been seen.

Tertiary front wall ultimately developed. The distal and proximal oral shields, above the secondary orifices, increase in size by the virtual sealing of the space directly above the orifice by a secondary plug of tissue. In addition, the huge, complete oral shields of adjacent zooecia join up by further accumulation of secondary calcareous tissue to form a very irregular cover pierced by deep *lacunae* and raised above the levels of the underlying frontal shields on the very stout stalks of the oral avicularia and on the ramifications of the distal oral shields. *Ovicells* not seen.

FIGS. 126–128. *Ubaghsia reticulata* (Ubaghs), D.1391. Labelled by Lang " *Batrachopora ornata* (Goldfuss) ".

(126) Adult zooecium and part of proximally adjacent zooecium. The tertiary front wall has been destroyed by wear.

(127) Adult zooecium with complete proximal oral shield supporting a fragment of tertiary front wall.

(128) Proximal oral shields. (*a*) Front view of orifice with broken proximal oral shield ; *fd*, fused distal oral spines ; *ia*, interzooecial avicularia ; *la*, lateral oral avicularia. (*b*, *c*) Side and top views respectively of orifice of adult zooecium with complete proximal oral shield ; *ab*, apertural bar ; *cp*, central plug of secondary tissue ; *fd*, fused distal oral spines ; *la*, lateral oral avicularia.

MEASUREMENTS. *Zooecia* Lz = 0·80 to 0·85 mm.
lz = 0·60 to 0·72 mm.
hr = 0·20 to 0·25 mm.
lr = 0·26 to 0·35 mm.
Avicularia Not measurable.

REMARKS. Voigt (1930 : 513) recognized that *Ubaghsia reticulata* (Ubaghs) and *Batrachopora hyla* Lang are synonymous. He stated "*Batrachopora hyla* Lang is merely a *Ubaghsia reticulata* in which the lamina peristomica [tertiary front wall] is missing" [translation]. Discussing other species of *Batrachopora*, he also remarked (1930 : 515) that "this [i.e., loss of the tertiary front wall in fossilization] is also true for other species, for example, in the case of the closely related *Batrachopora ornata* (Goldfuss), or even for the whole genus. But until there is more definite proof of this I retain the other species in *Batrachopora*" [translation].

Voigt's suggestions are here regarded as valid and the two genera are merged, for the frontal shields of *Batrachopora* and *Ubaghsia* are completely similar in structure, while the tertiary front wall was obviously loosely attached and easily lost in fossilization. Comparison of Jullien's figures (1886, pl. 18, figs. 4, 5) of *Ubaghsia reticulata* with D.1391, in which part of the tertiary front wall is preserved, make the synonymy particularly convincing.

See also remarks under *Ubaghsia ornata* (Goldfuss), (p. 263).

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian.

SPECIMENS. D.11852. Holotype of *Batrachopora hyla* Lang. Small fragment of zoarium, now unattached. Maastrichtian, Maastricht, Holland. van Breda Collection.

D.1391. Zoarial fragment labelled by Lang "*Batrachopora ornata* (Goldfuss)". Part of the tertiary front wall is preserved. Maastrichtian, Maastricht, Holland. G. R. Vine Collection.

D.40674–78. Five zoarial fragments labelled by Lang "*Batrachopora hyla*". Horizon, locality and collection as for D.11852.

12. ***Ubaghsia ornata*** (Goldfuss)

(Pl. 23, figs. 1–4 ; Text-fig. 129)

1826 *Cellepora ornata* Goldfuss, pp. 26, 248, pl. 9, fig. *1a, b*.
1828 *Cellepora ornata* Goldfuss : Morren, p. 34.
1832 *Cellepora ornata* Goldfuss : Dumont, p. 360.
1834 *Cellepora ornata* Goldfuss : von Klöden, pp. 266, 341, pl. 5, fig. 3.
1836 *Discopora ornata* (Goldfuss) Edwards, p. 253.
1846 *Cellepora ornata* Goldfuss : Geinitz, p. 612.
1848 *Cellepora ornata* Goldfuss : Bronn, p. 255.
1848 *Discopora ornata* (Goldfuss) : Bronn, p. 432.
1849 *Discopora ornata* (Goldfuss) : Bronn, p. 130.
1849 *Cellepora ornata* Goldfuss : Geinitz, p. 252.
1850 *Escharina ornata* (Goldfuss) d'Orbigny, p. 262.
1851 *Cellepora* (*Dermatopora*) *ornata* Goldfuss : von Hagenow, p. 98, pl. 10, fig. 16.
1851 *Cellepora* (*Dermatopora*) *ornata* Goldfuss : Bronn and Römer, p. 103 ; 1852, pl. 29^2, fig. 11 [copy of von Hagenow, 1851, pl. 10, fig. 16].

1853 *Semiescharipora ornata* (Goldfuss) d'Orbigny, p. 480.
1857 *Semiescharipora ornata* (Goldfuss) : Pictet, p. 112.
1862 *Cellepora ornata* Goldfuss : Goldfuss, p. 24, pl. 9, fig. 1*a*, *b*.
1879 *Cellepora ornata* Goldfuss : Quenstedt, p. 313, pl. 154, fig. 42.
1879 *Semiescharipora ornata* (Goldfuss) : Ubaghs, p. 217.
1881 *Semiescharipora ornata* (Goldfuss) : Mourlon, p. 116.
1885 *Cellepora ornata* Goldfuss : Vine, p. 161.
1885 *Cellepora* (*Dermatopora*) *ornata* Goldfuss : Vine, p. 164.
1889 *Semiescharipora ornata* (Goldfuss) : Ubaghs, p. 52.
1900*b* *Cribrilina* (*Costula*) *ornata* (Goldfuss) Canu, p. 450.
1916*a* *Batrachopora ornata* (Goldfuss) Lang, pp. 111, 112.
1916*a* *Cellepora ornata* Goldfuss : Lang, p. 169.
1919*d* *Batrachopora ornata* (Goldfuss) : Lang, pp. 205, 206, 217, 219, 221.
1921 *Batrachopora ornata* (Goldfuss) : Lang, p. xc.
1922 *Batrachopora ornata* (Goldfuss) : Lang, p. 370 [*partim*], text-fig. 117 [*non* pl. 8, fig. 4 = *Ubaghsia reticulata* (Ubaghs)].
1930 *non Batrachopora ornata* (Goldfuss) : Voigt, pp. 515, 543, 561, pl. 31, fig. 18.
1930 *Ubaghsia reticulata* (Ubaghs) : Voigt, p. 513 [*partim*], pl. 31, fig. 20, only—*non* fig. 19.

Lectotype. (Chosen by Lang, 1922 : 372). The specimen figured by Goldfuss, 1826, pl. 9, fig. 1*b*. Maastrichtian, St. Petersburg, near Maastricht, Holland.

Emended diagnosis. *Ubaghsia* with unbranched distal oral spines ; zooecia large (Lz = 1·00 to 1·25 mm., lz = 0·70 to 0·90 mm.) ; secondary orifice usually of equal height and width, as large as or larger than, the frontal shield ; costae massive, 3–7 (commonly 5), each with two lateral costal fusions and two very large pelmata ; avicularia of two kinds : (*a*) a very large lateral oral pair, (*b*) commonly paired, small, distally pointed interzooecial avicularia directed obliquely outwards from the zooecium they accompany.

Description. *Zoarium* unilaminar, probably encrusting. *Zooecia* broadly oval, very large. *Secondary orifice* very large, generally of equal height and width, as large as, or larger than, the frontal shield, rounded distally and laterally with a relatively straight proximal margin, or circular. The orifice is surrounded by complete distal and proximal oral shields. *Distal oral shield* probably formed by the amalgamation of the distal and distal-lateral pairs of oral spines. All the available specimens are generally worn, with only occasional zooecia with undamaged distal and proximal oral shields. Apparently the distal-lateral oral spines do not fuse on to the distal sides of the large oral avicularia as in *Ubaghsia reticulata*. *Proximal oral shield* formed by the very large, paired, lateral oral avicularia, which are raised on very thick stalks. The oral avicularia are distally pointed, proximally rounded and directed distally and obliquely inwards. They very probably fuse above the secondary orifice by the addition, mainly on their upper, inner sides, of secondary calcareous tissue. *Oral spines* 4, enlarged, unbranched, and immersed in much secondary tissue forming the distal oral shield. *Frontal shield* generally flat, transversely oval or longitudinally oval. Costae 3–7 (commonly 5), often very coarse and wide : the occurrence of only 3 very large costae in an adult zooecium of normal size is exceptional (D.8529). Each costa bears two very large *pelmata* at the levels of the *lateral costal fusions*, which are of variable thickness producing irregular *intercostal spaces*. Outwards from the very large proximal pelma each costa bends downwards abruptly to meet the *gymnocyst* which is apparently smooth but seldom visible. The *apertural bar* is about as wide as the costae, straight or slightly concave, and carrying two large pelmata which may be confluent in one large depression.

Avicularia of two kinds : (*a*) a very large lateral oral pair, one on either side of, and close to, the lateral margins of the orifice, (*b*) a small, commonly paired interzooecial form. Avicularia of type (*a*) are proximally rounded and distally pointed, directed distally and obliquely inwards, raised on much thickened stalks, and probably connected by a bar-like accumulation of secondary tissue between them.

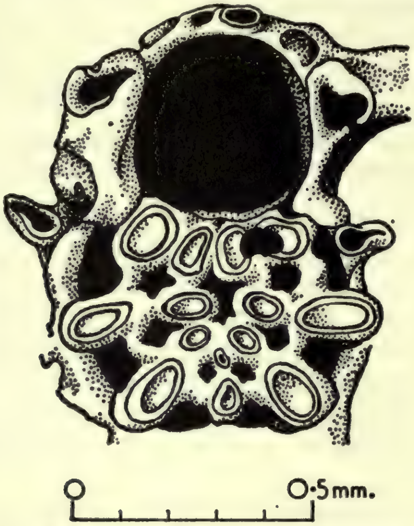

FIG. 129. *Ubaghsia ornata* (Goldfuss). D.19356. Labelled by Lang " *Batrachopora ornata* (Goldfuss) ". Adult zooecium with typically very large orifice and two pointed interzooecial avicularia. The proximal oral shield and tertiary front wall destroyed by wear.

Avicularia of type (*b*) are much smaller, commonly paired, one near each end of the apertural bar and a little proximally to it ; they are pointed, rounded proximally and directed distally and obliquely outwards from the zooecium they accompany. These small interzooecial avicularia are often worn and partly obscured by secondary tissue expanding from the proximal oral shield. *Tertiary front wall* probably present and formed as in *Ubaghsia reticulata*, but eroded in the specimens available. *Ovicells* not seen.

MEASUREMENTS. *Zooecia* Lz = 1·00 to 1·25 mm.
lz = 0·70 to 0·90 mm.
hr = 0·40 to 0·42 mm.
lr = 0·40 to 0·45 mm.
Lateral oral avicularia Lz = 0·16 mm.
lz = 0·10 mm.
Interzooecial avicularia Not measurable.

REMARKS. Lang (1922 : 372) emphasized the importance of the distal and proximal oral shields as distinguishing features of the species, and compared the distal shields with those of *Ichnopora denticulata.* He figured (1922, pl. 8, fig. 4), as representative of *Ubaghsia ornata,* four zooecia of D.1391, which is a fairly well-preserved zoarial fragment retaining part of its tertiary front wall. This specimen clearly belongs to *Ubaghsia reticulata* (Ubaghs), for its measurements and other characters agree with those of that species and differ consistently from those of the other specimens (D.8529, D.19356–57) which Lang also placed in *ornata.* I agree that the last three specimens should be retained in *Ubaghsia ornata.*

Ubaghsia ornata (Goldfuss) is distinguished from *U. reticulata* (Ubaghs) by its fewer costae, its pelmata (which are equal in number to the lateral costal fusions), its larger zooecia, and its larger and differently shaped orifice. In addition, the lateral oral and interzooecial avicularia of *U. ornata* differ from those of *U. reticulata.* The species can be distinguished without placing too much reliance on the characters of the distal and proximal oral shields ; not only are these structures easily eroded, but they may also vary considerably in form and size, depending on the amount of secondary tissue accumulated round them. The tertiary front wall is extremely variable and irregular, and is seldom preserved at all in the material available ; it is of diagnostic value generically but does not aid in separation of the species.

D.28526 is doubtfully assigned to *U. ornata.* The measurements and other characters of three of the complete adult zooecia in the specimen (e.g., Lz, lz and the number of lateral costal fusions) are more in accord with those of *U. ornata* than with those of *U. reticulata.* But the dimensions of the orifice (hr = 0·30 mm., lr = 0·35 mm.) are generally smaller than those of *U. ornata* and it is somewhat wider than high.

Ubaghsia ornata (Goldfuss) and *U. reticulata* (Ubaghs) are closely related but distinguishable species. As yet they have been recorded only from the Maastrichtian of Maastricht.

Lang (1922 : 365) has suggested that they were derived respectively from *U. crassa* and *U. ranunculus,* two species described by him from the Rügen Chalk. Apart from the possibility that the Rügen horizon of these specimens is equivalent to the littoral Maastrichtian of the type area, the geographical relationship of the two areas makes such a relationship very unlikely.

If Lang's suggested lineages for *Ubaghsia ornata* and *U. reticulata* are not accepted, it does not mean that the " alternative hypothesis " mentioned by him (1922 : 366), that *U. ornata* is derived from *U. reticulata,* must be adopted. There is no evidence to decide whether *U. ornata* developed from *U. reticulata* or vice versa.

STRATIGRAPHICAL DISTRIBUTION. Maastrichtian.

SPECIMENS. D.8529. A large zoarial fragment, now unattached, labelled by Lang " *Batrachopora ornata* (Goldfuss) ". Maastrichtian. Fauquement, east of Maastricht, Holland. W. Gamble Collection.

D.19356–57. Two zoarial fragments, now unattached, labelled by Lang " *Batrachopora ornata* (Goldfuss) ". Maastrichtian. Maastricht, Holland. G. R. Vine Collection.

?D.28526. A fragmentary zoarium, labelled by Lang "*Batrachopora ornata* (Goldfuss)". Horizon, locality and collection unknown, but very probably Maastrichtian of Maastricht, Holland. [The specimen is here only doubtfully assigned to *Ubaghsia ornata* (Goldfuss).]

SPECIES OF UNCERTAIN SYSTEMATIC POSITION PREVIOUSLY ASSIGNED TO *BATRACHOPORA*

(1) ***Cellepora (Discopora) signata*** von Hagenow

1851 *Cellepora* (*Discopora*) *signata* von Hagenow, p. 96, pl. 10, fig. 17*a*, *b*.

REMARKS. Although Lang (1922 : 361) chose the specimen figured by von Hagenow as lectotype, he also remarked "from the evidence available, it is impossible to diagnose this species or more than tentatively to refer it to *Batrachopora*". There is no evidence to suggest it might be a *Batrachopora*; the genus and species are indeterminate.

(2) ***Semiescharipora ovalis*** d'Orbigny

1852 *Semiescharipora ovalis* d'Orbigny, pl. 719, figs. 13–16.
1853 *Semiescharipora ovalis* d'Orbigny : d'Orbigny, p. 488.
1854 *Semiescharipora ovalis* d'Orbigny : d'Orbigny, p. 1098.

REMARKS. Lang (1916*a* : 110, 111) placed *Semiescharipora ovalis* d'Orbigny in *Batrachopora* and later (1922 : 367) selected the specimen figured by d'Orbigny (1852, pl. 719, fig. 14) as lectotype. Again there is no definite evidence to suggest that the material figured by d'Orbigny or described by him (1853 : 488) belongs to *Batrachopora*. Canu (1900*b* : 457) has listed the species as worn and doubtful. All that may be deduced with certainty from the figure and description is that *Semiescharipora ovalis* d'Orbigny is a cribrimorph polyzoan from the Maastrichtian of Royan. It has a well-developed frontal shield with fairly numerous costae and lateral costal fusions, and paired, large, lateral oral avicularia.

(3) ***Reptescharipora convexa*** d'Orbigny

1852 *Reptescharipora convexa* d'Orbigny, pl. 720, figs. 1–3.
1853 *Reptescharipora convexa* d'Orbigny : d'Orbigny, p. 492.
1854 *Reptescharipora convexa* d'Orbigny, : d'Orbigny, p. 1098.

REMARKS. Lang (1916*a* : 111, 112) regarded *Reptescharipora convexa* d'Orbigny as a species of *Batrachopora* and later (1922 : 368) selected the specimen figured by d'Orbigny (1852, pl. 720, fig. 2) as lectotype.

There is, if anything, even less evidence for regarding *Reptescharipora convexa* as a *Batrachopora* than in the case of *Semiescharipora ovalis* d'Orbigny. It is a cribrimorph polyzoan, from the Senonian of Meudon, with apparently about 10 costae and about 5 lateral coatal fusions. The paired lateral oral avicularia are not large. Canu (1900*b* : 449) referred the species to *Cribrilina*. He gave the dimensions of the species as Lz = 1·00 to 1·14 mm., lz = 0·57 to 0·71 mm., hr = 0·17 to 0·22 mm., lr = 0·28 mm., and mentioned the occasional presence of two marginal [oral] spines.

(4) ***Batrachopora royanensis*** Lang

1916*a* *Batrachopora royanensis* Lang, pp. 110, 111.
1919*d* *Batrachopora royanensis* Lang : Lang, pp. 205, 206, 221.
1922 *Batrachopora royanensis* Lang : Lang p. 374, text-fig. 118.

REMARKS. Lang (1916*a*) based his diagnosis of this species on a photograph of the holotype, which is in the F. Canu Collection. It can be seen from the photograph that the orifices of the zooecia are much smaller than the frontal shields, wider than high, rounded distally with straight sides, which begin to converge proximally, and with a straight proximal margin. There are apparently no lateral oral avicularia. Apparently 12–14 costae are present, each with at least two lateral costal fusions and pelmata and pelmatidia. The number of oral spines is indeterminate. Interzooecial avicularia of two kinds appear to be present : (*a*) a small, rounded, paired form just distal to each orifice, (*b*) a larger, laterally constricted, occasional, sporadic form of uncertain shape and orientation. Ovicells cannot be seen. There is no indication that the zoarium is necessarily " erect [and] bilaminar " as Lang (1922 : 374) has stated.

There is not sufficient evidence to place the specimen with certainty in any cribrimorph genus. It is clear, however, that the specimen lacks the large, well-defined, lateral oral avicularia characteristic of *Batrachopora*, and that its frontal shield is different from those of species of *Ubaghsia* (which here includes *Batrachopora*).

(5) ***Batrachopora ultima*** Voigt

1925*b* *Batrachopora ultima* Voigt, pp. 99, 103, pl. 3, figs. 7, 8 ; text-fig. 4.
1930 *Batrachopora ultima* Voigt : Voigt, pp. 515, 561, pl. 31, fig. 16 (copy of part of pl. 3, fig 8, 1925*b*).
1939 *Batrachopora ultima* Voigt : Voigt, p. 93, text-fig. 4*c*.

REMARKS. Voigt (1925*b* : 103) described the species as follows : " zoarium unilaminar, erect. Zooecia arranged in regular quincuncial lines, elongate-oval, sometimes twice as long as broad but usually somewhat shorter. The ' anterior wall ' is formed only from the frontal shield, which, on the average, consists of from 7–10 exceptionally broad costae which fuse laterally and at their inner ends along the mid-line. Thus the frontal shield is pierced generally by 4, or more rarely 5, regular, parallel, transverse, rows of pores [intercostal spaces], usually 3 or 4 to a row. The broad ' prolongations ' [outermost ends] of the costae alternate at the margin [of the frontal shield] with the narrower inter[-costal] spaces. Under the microscope, delicate ' vertically crossing ' lines may be seen on the costae. *Pelmata were presumed in view of the ' sporadic punctures '* [?pores or intercostal spaces] *rather than observed ; the figure* [Voigt, 1925*b*, text-fig. 4] *is to be considered in this light.*[1] Orifice semicircular . . . surrounded usually by 5 [oral] spines. In all probability there is a small, elongate avicularium on either side of the orifice. I consider this to be the case because of the small protuberances on either side of the orifice, each of which seems to have possessed a pore. Several other species of *Batrachopora* support this, as they always have avicularia on either side of the orifice. *But I have*

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[1] My italics.

not observed the avicularia for certain because of the condition of preservation of the specimen.[1]

" *Batrachopora ultima* is the youngest *Batrachopora*. *B. crassa* Lang is similar (also with about 7 costae) but it is distinctly larger (1·25 mm.). *B. perforata* (Marsson), from Rügen, which is distinguished by two large lateral avicularia, is more distantly related " [translation].

It is apparent that Voigt described *B. ultima* without fully determining the character of the frontal shield, particularly the presence or absence of definite pelmata. He also seemed uncertain of the nature of the oral avicularia, or even whether they were present or not.

I do not accept *B. ultima* Voigt as a definite species of *Ubaghsia*, because of the uncertainty of the true character of the type material. There is one specimen, D.31990, in the British Museum (Natural History), presented by Prof. E. Voigt, and labelled by him " *Batrachopora ultima* Voigt, Daniendrift, Blaue Berge, near Rosslau, Anhalt ". This specimen is a cribrimorph polyzoan with frequent, prominent, hyperstomial ovicells, and is quite unlike any species of *Batrachopora* [=*Ubaghsia*]. Lang's label with the specimen shows that he doubtfully retained it in *Batrachopora*.

(6) ***Escharoides peltata*** Roemer

1840 *Escharoides peltata* Roemer, p. 14, pl. 5, fig. 7.

REMARKS. Lang (1916 : 410 ; 1921 : 13) has already listed this as a species of doubtful systematic position. However, Voigt (1949 : 41, pl. 10, figs. 4, 5) recorded *Batrachopora* [*Escharoides*] *peltata* (Roemer) from the Senonian, zone of *G.* [*A.*] *quadrata* of Oberg and Misburg, Hanover, Germany. I do not agree with Voigt's placing of his specimens as a species of *Batrachopora*. Roemer's figure is difficult to interpret, and Voigt's very clear figures (1949, pl. 10, figs. 4, 5) show a species which may belong to *Escharoides peltata* Roemer, but definitely not to *Batrachopora* Lang.

Genus ***ANDRIOPORA*** Lang

1921 *Andriopora* Lang, p. 89—for earlier references.

The new species described below are assigned to *Andriopora* which has not been completely revised. The described material has been compared with all available specimens of *Andriopora* in the collections of the British Museum (Natural History).

1. ***Andriopora minor***[2] sp. nov.

(Pl. 23, fig. 6 ; Text-fig. 130)

HOLOTYPE. D.39417. Zoarial fragment encrusting the dorsal surface of a fragment of a unilaminar zoarium of *Pelmatopora* cf. *palmata* Lang. Senonian, zone of *G.* [*A.*] *quadrata*. Pit 17 of Gaster, large pit, in two sections, in Cote Bottom, Durrington, Sussex.

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[1] My italics.

[2] With reference to the small size of the zooecia.

DIAGNOSIS. *Andriopora* with small, elliptical, non-caudate zooecia ; orifice wider than high ; oral spine-bases 6 ; costae 15–20, each with about 4 lateral costal fusions ; apertural bar unmodified ; gymnocyst narrowly exposed round the frontal shield ; avicularia generally paired.

DESCRIPTION. *Zoarium* encrusting, uniserial, tending to appear multi-serial through an irregular decrease in the angle of branching and through the tendency for different series of zooecia to overlap. *Zooecia* small, elliptical, non-caudate. *Orifice* wider than high, rounded distally and laterally or tending to be straight-sided, proximal margin straight. *Oral spine-bases* 6, very minute, hardly visible. *Frontal shield* well arched, slightly flattened on top. *Costae* 15–20, very narrow, with a variable number, often 4, very fine *lateral costal fusions*. There are no median pores or slits on the costae, nor do the costae tend to be up-turned at their inner ends. *Median area of fusion* narrow. *Apertural bar* unmodified, but tending to be somewhat wider than the costae. *Gymnocyst* narrowly exposed laterally, and more widely exposed proximally to the frontal shield and round the avicularia.

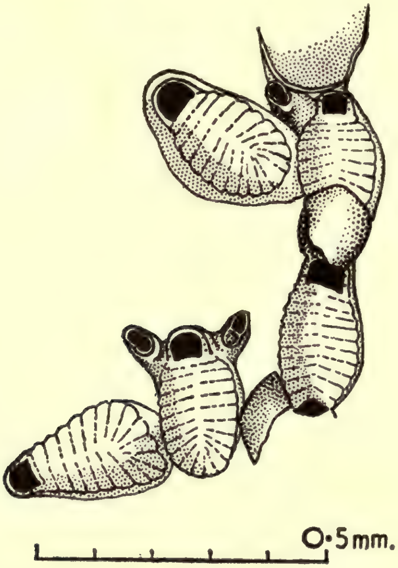

FIG. 130. *Andriopora minor* sp. nov. D.39417. Holotype. Five zooecia ; one with single avicularium and one with paired avicularia. One zooecium with slightly damaged ovicell.

Avicularia large, prominent, paired, one just beyond each distal lateral margin of the orifice, or occurring singly on one side or the other, directed distally away from the mid-line of the orifice they accompany. The avicularian aperture is elongate-oval, or tending to be pointed distally, and is divided by a narrow *transverse bar* into a more-or-less triangular *rostrum*, and a wider, semicircular proximal portion.

Ovicells hyperstomial, very prominent, large, globular, smooth, somewhat compressed laterally and standing up above the zooecium on which they are developed.

MEASUREMENTS. *Zooecia* Lz = 0·27 to 0·33 mm.
lz = 0·15 to 0·18 mm.
hr = 0·035 mm.
lr = 0·060 mm.
Avicularia Lz = 0·06 mm.
lz = 0·03 mm.

REMARKS. *Andriopora minor* is characterized by its small size and its closely placed non-caudate zooecia. The oral spine-bases are very minute and not at all thickened.

STRATIGRAPHICAL DISTRIBUTION. Senonian, zone of *G.* [*A.*] *quadrata*.

SPECIMENS. D.39417. Holotype—see above.

2. *Andriopora major*[1] sp. nov.

(Pl. 23, fig. 5; Text-figs. 131, 132)

HOLOTYPE. D.39418. Small zoarial fragment encrusting a piece of echinoid test. Senonian, zone of *B. mucronata*. Norwich, Norfolk. A. W. Rowe Collection.

DIAGNOSIS. *Andriopora* with large, widely elliptical zooecia, each with a long narrow cauda; orifice higher than wide, with proximal-lateral constrictions; oral spine-bases 6, prominent, somewhat thickened; costae 15–19, without lateral costal fusions; apertural bar sharply bent proximally; gymnocyst well exposed; avicularia apparently absent.

DESCRIPTION. *Zoarium* encrusting, uniserial, the angle of branching is apparently maintained, keeping the individual series of zooecia clearly separate. *Zooecia* broadly elliptical, with long, straight *caudae*. *Orifice* higher than wide, rounded distally and laterally with proximal-lateral constrictions, the proximal margin "U"-shaped. *Oral spine bases* 6, somewhat enlarged, tending to be arranged laterally in two groups of three. *Frontal shield* well arched. *Costae* 15–19 (occasionally 13), usually fairly wide. No *lateral costal fusions*. The inner ends of the costae are not up-turned near the mid-line, nor are any pores or costal slits visible. *Median area of fusion* fairly wide. *Apertural bar* with rounded outer ends, narrowed and bent proximally along the mid-line, otherwise not flattened in a vertical plane nor substantially thickened. *Gymnocyst* widely exposed laterally and particularly proximally to the frontal shield where it is prolonged into a straight, rapidly tapering, narrow *cauda*. The gymnocyst also appears on either side of the orifice and tapers rapidly distally giving a rounded distal margin to the zooecium from which the cauda of the distally adjacent zooecium often arises.

Avicularia not seen. There is no evidence of broken avicularia or other heterozooecia, and avicularia are presumed absent in this species. *Ovicells* hyperstomial, globular, smooth, apparently somewhat compressed laterally.

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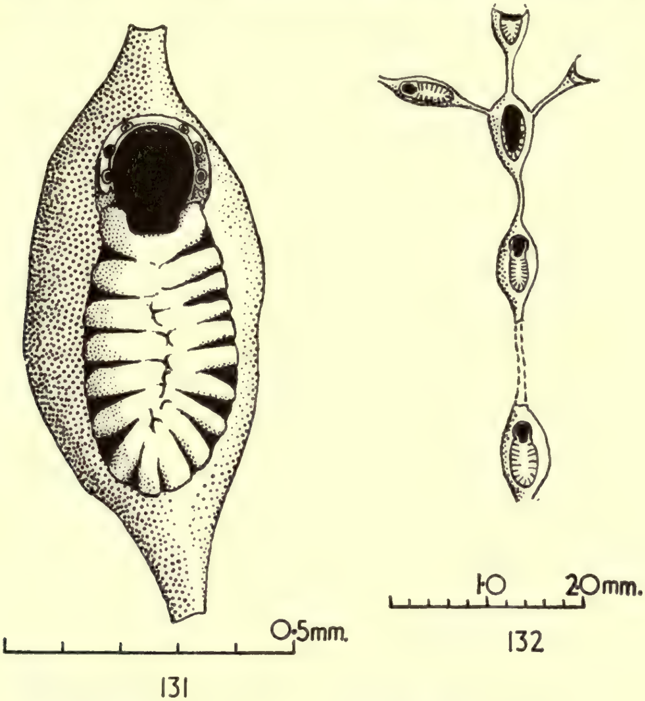
[1] With reference to the unusually large size of the zooecia.

Measurements. *Zooecia* Lz = 0·72 mm.
lz = 0·42 mm.
hr = 0·15 to 0·18 mm.
lr = 0·12 mm.
Lc = 0·33 to 0·50 mm.
lc = 0·02 mm.

Remarks. The large size of the zooecia, the widely exposed gymnocyst, and the apparent absence of avicularia are particularly distinctive characters of *Andriopora major*. The orifice is more complex than in *A. minor* and the oral spine-bases more distinct than in that species. The ovicells of *A. major* are described from one broken example present on an isolated zooecium.



Figs. 131, 132. *Andriopora major* sp. nov. D.39418. Holotype.
(131) Single adult zooecium ; the cauda worn away.
(132) Part of zoarium showing mode of branching and long, straight, narrow caudae.

Stratigraphical distribution. Senonian, zone of *B. mucronata*.

Specimen. D.39418. Holotype—see above.

VIII. SYSTEMATIC BASIS, STRATIGRAPHY AND EVOLUTION OF THE GENERA AND SPECIES REVISED

Recognition of distinct species in the Cretaceous cribrimorph Polyzoa is made difficult by the wide variation in morphology which may occur between adult zooecia of the same and different zoaria of a single species, and between young and adult zooecia of a single zoarium. It is important to assess this range of variation, especially as Cretaceous cribrimorph polyzoan colonies are often broken, so that the extremes of variation—originally part of the same zoarium—become separated and form apparently distinct species. This fragmentation also gives a false idea of the abundance of a particular species at any one horizon or locality.

The present assessment of the species-unit in Cretaceous cribrimorph Polyzoa is an attempt to use all available zooecial characters rather than distinguishing species by the modifications which may be apparent in any one character. Divisions based solely on measurements of the length and width of zooecia, or on zoarial growth habit alone, have been avoided, and, generally, where Lang has distinguished species by these methods they have proved to be synonymous.

In addition to comparative morphology Lang used stratigraphical and astogenetic " criteria of relationship " in his systematic assessment of species. Thus species which differ only very slightly in one or more characters were maintained as distinct if they occurred at well-separated horizons. Species may be maintained on this basis when little material is available for study. The principle has been followed to some extent in the present revision, with the reservation that the slight, but distinct, differences must be essentially structural rather than incidental differences in size or growth habit.

The astogenetic basis on which Lang occasionally distinguished some species has not been followed. He generally used astogenetic differences as indications of the possible course of evolution.

As several of the species established by Lang are here merged it has been necessary to revise the stratigraphical ranges of some species, and the large amount of new material examined has extended the known ranges of most species.

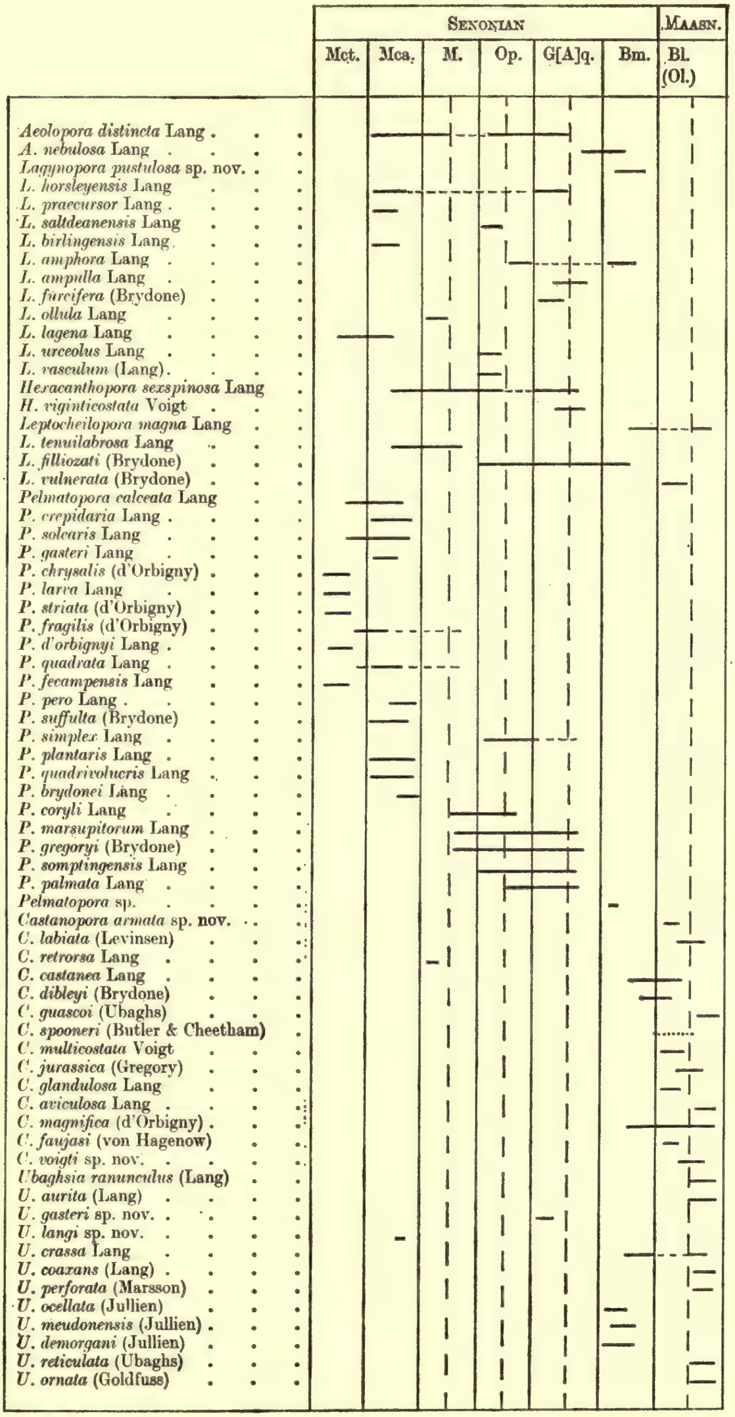
The stratigraphical ranges of the species revised and described here are shown in the accompanying distribution table and discussed subsequently. The range of some species is shown in parts as a broken line indicating that the species has not yet been recorded from that horizon, but that it is thought to range through.

Lang's very extensive studies (1916*a*, *b*, 1919*a–d*, 1921, 1922, 1925, 1929) of Cretaceous Polyzoa, and other groups, led him to adopt an orthogenetic view of evolution, formulated in what has since been termed the " Theory of Trends ". This concept required that, by means of an internal compulsive force, groups of related organisms may follow a predetermined and irreversible course of evolution to a pitch of disharmony with their environment, developing apparently functionless structures ; and that they may undergo periodic, parallel evolution or recapitulation independent of environmental effects. Lang applied this vitalist view of evolution to the Cretaceous cribrimorph Polyzoa (1919*c* : 105 ; 1919*d* : 196 ; 1921 : xvii ; 1922).

This application of the Theory of Trends produced much lively criticism which laid increasing emphasis on environmental adaptations as a more acceptable explanation of the apparent sequence of evolutionary changes (e.g., Bather, 1921 : 18 ; Brydone, 1929 : 6 ; Withers, 1935 : 8).

In the genera revised here, and in other genera of Cretaceous cribrimorph Polyzoa, evolution in the detailed sequence of forms has taken place in a diverging plexus of

Stratigraphical Distribution of Genera and Species Revised



variation, rather than along the confined and determinate, distinct lines of development which Lang has postulated. The present revision merges several of the species, and some genera, recognized by Lang so that his suggested detailed, and even more general, lines of evolution break down. This is particularly so in the case of *Pelmatopora.*

AEOLOPORA

Two species, *A. distincta* and *A. nebulosa,* are here regarded as comprising the genus. By an increase in zooecial size, a thickening of the apertural bar, a slight reduction in the number of costae and an apparent loss of avicularia *A. nebulosa* has evolved from *A. distincta.* The stratigraphical occurrence of both species is discussed on p. 64.

LAGYNOPORA

The stratigraphical ranges of the twelve species of *Lagynopora* recognized here are almost all brief. Only *L. horsleyensis* is recorded from the zone of *M. coranguinum* as well as from the zone of *G.* [*A.*] *quadrata,* and no specimens are as yet recorded from the intervening zones. *L. pustulosa* sp. nov. is stratigraphically the highest species known from the Senonian.

The evolutionary relationships of the twelve species are uncertain. Probably *L. horsleyensis* may be excluded from the main plexus of evolution of the genus as it is the only species with lateral costal fusions. Similarly the small zooecia and other distinctive characters of *L. saltdeanensis* and *L. pustulosa* suggest that the evolution of these two has been somewhat different from that of the remaining nine species of *Lagynopora.* These are generally related, but it is very uncertain that the individual lineage linkages shown by Lang (1921 : 54) are correct.

HEXACANTHOPORA

Only two species are recognized here ; *H. sexspinosa,* from the zones of ?*M. coranguinum* to *G.* [*A.*] *quadrata* of the English Chalk, and *H. viginticostata* from the zones of *G.* [*A.*] *quadrata* and *B. mucronata* in Germany. *H. sexspinosa* is not yet recorded from the *Echinocorys scutata* var. *cincta* zubzone of the zone of *O. pilula.*

H. viginticostata may have evolved from *H. sexspinosa* by an increase in the number of costae, a marked widening of the median area of fusion, and by a reduction in the number and type of avicularia.

LEPTOCHEILOPORA

Only four species are recognized here. *L. tenuilabrosa* is the earliest, and *L. filliozati* has the longest range in the Senonian and is represented by the greatest number of specimens. *L. magna* ranges from the Senonian, zone of *B. mucronata,* in England, to the Lower Maastrichtian, in Germany, but is not yet recorded from the Chalk with *Ostrea lunata* in England. *L. vulnerata* is known from only three specimens, one from the Senonian, zone of *B. mucronata,* and two from the Lower Maastrichtian, zone of *Belemnella lanceolata,* from the Chalk with *Ostrea lunata.* *Leptocheilopora* is unrecorded from the upper part of the zone of *Marsupites.*

The sequence *L. tenuilabrosa–L. filliozati–L. vulnerata* probably indicates the main course of evolution in the genus. There is a slight reduction in zooecial size and in the number of costae and a loss of avicularia. By contrast, there is an increase in the number of oral spines from four in *L. tenuilabrosa* and *L. filliozati* to seven in *L. vulnerata*. The structure of the ovicell is simplified from the costate type in *L. tenuilabrosa* to more usual smooth ovicells in the remaining species. In *L. magna*, the youngest species of the genus, there is a pronounced increase in zooecial size and very marked proximal-lateral constrictions in the orifice. The four oral spine bases are very small, but, like the preceding species, there are no avicularia. *L. magna* possibly diverged from the main course of evolution in early *B. mucronata* times.

PELMATOPORA

Lang (1922 : 242) has stated that " though almost certainly arising in the Turonian (since *Sandalopora*, an obvious derivative, has occurred in the Turonian of France) the earliest known forms of *Pelmatopora* are found at the base of the Senonian, and immediately appear in great numbers both of species, and in some species, of individuals ". While it is true to say that several species of *Pelmatopora* make an abrupt appearance at the base of the Senonian it is an overstatement that they are present in great numbers. They occur frequently, but they are by no means so abundant as in the upper part of the Senonian, particularly in the zones of *O. pilula* and *G.* [*A.*] *quadrata*.

The twenty-two species of *Pelmatopora* recognized here fall stratigraphically into two well-defined groups. There is an early Senonian development in the zones of *M. cortestudinarium* and *M. cor-anguinum* of sixteen species, which, with the exception of *P. brydonei* and *P. quadrivolucris*, all have unmodified oral spine-bases. A second, very abundant, group of six species characterizes the higher Senonian zones of *Marsupites* to *G.* [*A.*] *quadrata*. With the exception of *P. simplex*, these all have modified and enlarged distal oral spines. No species of *Pelmatopora* are yet recorded definitely from the *Uintacrinus* Subzone of the *Marsupites* Zone. Recently a definite *Pelmatopora* specimen has been recorded from the Danian of Herfølge, Denmark (see p. 202).

The ranges of certain species of *Pelmatopora* are apparently limited within some zones of the Senonian. Thus *P. pero* and *P. brydonei* are recorded only from the upper part of the zone of *M. cor-anguinum*, while *P. calceata*, *P. crepidaria*, *P. solearis*, *P. gasteri*, *P. fragilis*, *P. quadrata*, *P. suffulta*, *P. plantaris* and *P. quadrivolucris* are most frequent in the lowest quarter of the same zone. *P. chrysalis*, *P. larva*, *P. striata*, *P. d'orbignyi* and *P. fecampensis* apparently characterize the middle part of the zone of *M. cortestudinarium*. *P. simplex* occurs frequently in the zone of *O. pilula*. The remaining five species of *Pelmatopora* are very abundant from the upper part of the zone of *Marsupites* to the upper part of the zone of *G.* [*A.*] *quadrata*, but, unlike the earlier Senonian species, they do not appear to be limited to distinct horizons of these zones.

The broad course of evolution in *Pelmatopora* may be summarized as a development from a Lower Senonian group of smaller, less complex, species with unmodified oral spine bases to an Upper Senonian group of larger, more complex, species with modified, enlarged distal oral spines. Several of the species which Lang recognized in the higher group are synonymous. The almost total absence of *Pelmatopora* species in the *Uintacrinus* Subzone of the *Marsupites* Chalk, and in fact the general absence of Polyzoa and other fossils at this level in the Senonian, may correlate with contemporary deeper water conditions. Calcareous shells of other organisms, such as echinoids and lamellibranchs, are noticeably scarce in the *Uintacrinus* Chalk thus reducing the occurrence of substrates suitable for polyzoan growth. Where larger shelled organisms are more abundant there is a clearly marked increase in the polyzoan fauna. Such an effect would account for the apparent periodicity of evolution which Lang regarded as having occurred during the development of *Pelmatopora*.

The suggested evolution from *P. pero* of the higher group of more complex *Pelmatopora* species (Lang, 1922 : 250) seems less likely than the course of evolution indicated here. *P. quadrivolucris* and *P. brydonei*, in contrast to other species of the Lower Senonian group, both possess distinctly enlarged oral spines and more complex frontal shields, therefore I regard them as fore-runners of the Upper Senonian group of *Pelmatopora* species in which the distal oral spines form a prominent distal oral shield.

P. simplex, which lacks enlarged distal oral spines, is the only species of its kind above the zone of *Marsupites*. Within the Upper Senonian group of more complex species there was, apparently, a tendency to evolve increasingly larger, flatter and more bifurcated distal oral spines. *P. palmata*, in which this tendency is most marked, is closely related to the species-group of *P. marsupitorum*, *P. gregoryi* and *P. somptingensis*.

CASTANOPORA

Fourteen Cretaceous species of *Castanopora* are described here. Only one of these, *C. retrorsa*, represented by an isolated specimen from the *Uintacrinus* Subzone of the *Marsupites* Zone, occurs below the top part of the zone of *B. mucronata*. All other species are of Maastrichtian age—many coming from the boreal Maastrichtian of Rügen. *C. castanea*, *C. dibleyi* and *C. magnifica* have been recorded from the Senonian, zone of *B. mucronata*, but are more common in the Maastrichtian, in the zone of *Belemnella lanceolata* (*Ostrea lunata* Chalk) in England, and in that zone abroad. The appearance of several new species of *Castanopora* in the *Ostrea lunata* Chalk of Trimingham, Norfolk, is a significant indicator of the general faunal change, shown particularly by the foraminifera at this level, between the Senonian, and the Maastrichtian.

Canu & Bassler (1933 : 53, 54) have assigned two species from the Vincentown Limesand to *Rhiniopora* thus extending the upward range of the genus into the Palaeocene.

The main evolutionary spread of *Castanopora* took place at the close of the Senonian, so that *Castanopora* characterizes the Lower Maastrichtian. The species recognized exhibit considerable variation in the number and type of avicularia.

UBAGHSIA

Twelve species of *Ubaghsia* are recognized here. Of these, only *U. gasteri* sp. nov. and *U. langi* sp. nov. occur below the zone of *Belemnitella mucronata*. There is a marked increase in the number of species in the Maastrichtian, most specimens coming either from the boreal Maastrichtian of Rügen, or from the littoral Maastrichtian of Maastricht, Holland.

The two new species, *U. gasteri* and *U. langi*, from the English Senonian (zones of *G.* [*A.*] *quadrata* and *M. cor-anguinum* respectively), extend the downward range of the genus. All the material previously described by Lang, and Jullien's original specimens, were from continental localities, either from the Senonian zone of *Belemnitella mucronata* of Meudon [*U. meudonensis* and *U. demorgani*] and Port Brehay [*U. ocellata*], or from the boreal Maastrichtian of Rügen [*U. perforata, U. ranunculus, U. crassa* and *U. coaxans*], from the littoral Maastrichtian of Maastricht [*U. ornata* and *U. reticulata*], and from Royan, France [*U. aurita*].

The later species of *Ubaghsia* fall into two main groups. *U. ranunculus, U. aurita, U. crassa, U. coaxans* and (?) *U. perforata* all lacking the very heavy tertiary front wall which characterizes the other group of *U. ocellata, U. meudonensis, U. demorgani, U. reticulata* and *U. ornata*. There is some indication that the marked accumulation of calcium-carbonate, in the tertiary front walls of the second group, may be related to habitat. As with some Cretaceous cirripedes (Withers, 1935 : 11, 13) there seems to be some correlation between a shallow water habitat and marked skeletal development of calcium-carbonate, since the species of the second group occur in littoral Maastrichtian sediments of the type locality, but other species from the boreal Chalk of Rügen are noticeably less robust.

It is thus evident, from the material revised here alone, that the Cretaceous cribrimorph polyzoan faunas of the Chalk contain a number of species and genera with well-marked stratigraphical ranges. Some species apparently have a limited range within the existing recognized zones. Some division of the very thick zones of *M. cor-anguinum* and *B. mucronata* should be possible, on the basis of their contained cribrimorph polyzoan faunas, when further systematic revision of other genera is completed and when new material has been examined from collections made more recently.

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PLATE 1

Aeolopora distincta Lang

FIG. 1. Group of adult zooecia, some ovicelled (*o*), interzooecial avicularium present (*a*). Holotype. ×30. D.28062.

FIG. 2. Group of adult zooecia. Holotype of *A. stellata* Lang. ×30. D.28911.

FIG. 3. Group of adult zooecia showing particularly the form of the apertural bar and interzooecial avicularia (*a*). Holotype of *A. stellata* Lang. ×30. D.28911.

FIG. 4. Group of adult zooecia. × 30. D.40654.

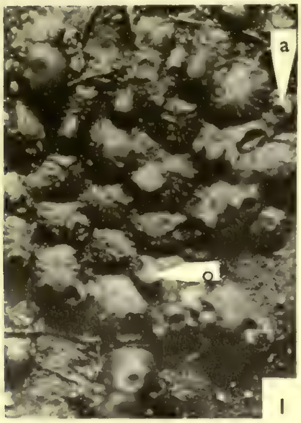
FIG. 5. Group of adult zooecia with a cluster of heterozooecia (*h*). ×30. D.40658.

FIG. 6. Group of adult zooecia, some with six oral spine bases (*o.s.*). ×30. D.40657.

FIG. 7. Group of adult zooecia, some ovicelled, showing prominently the " rings " of boss-like pelmatidia (*p*). Paratype. ×30. D.28061.

FIG. 8. Adult zooecia, the ovicell with small lateral slits (*l*). ×100. D.40599.

FIG. 9. Adult zooecia, showing the median ridge on the ovicell in the centre. ×100. D.40653.



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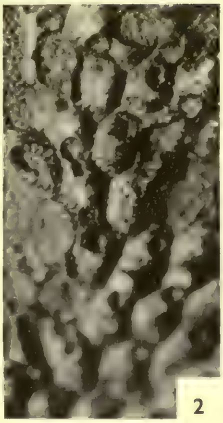

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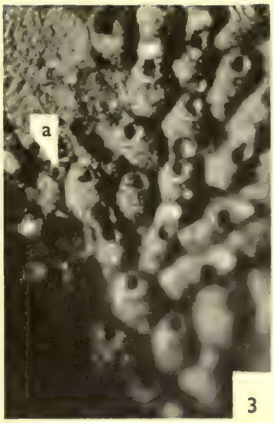

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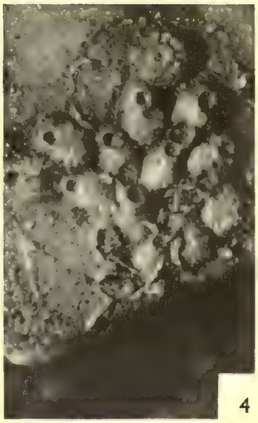

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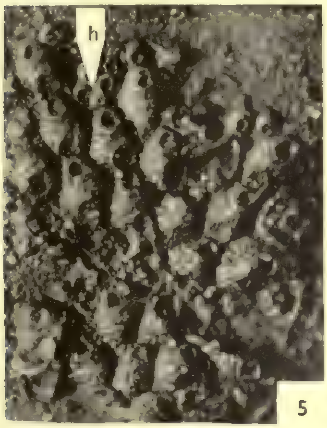

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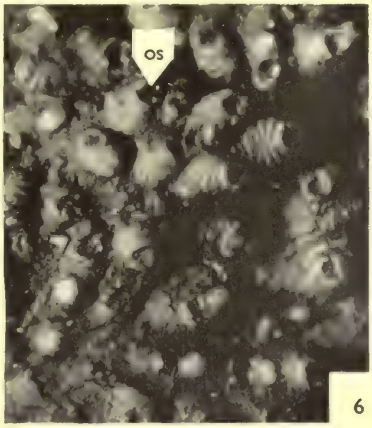

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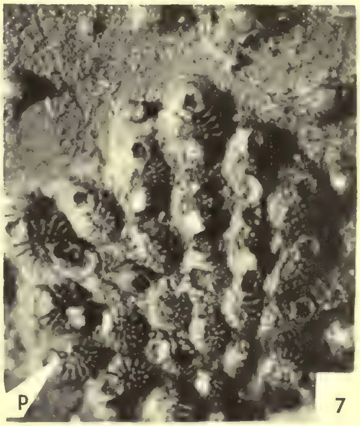

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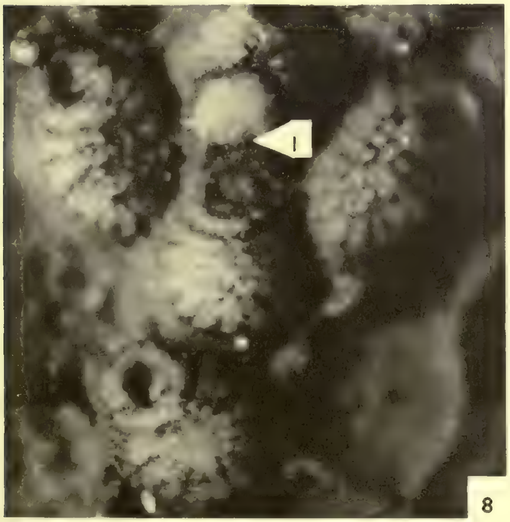

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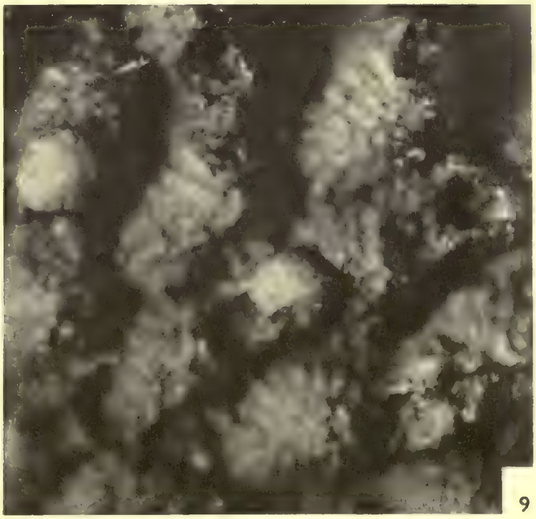


9

AEOLOPORA

PLATE 2

Aeolopora distincta Lang

FIG. 1. Part of a zoarium with the zooecia budded in long lines. × 30. D.40653.

FIG. 2. Group of adult zooecia, showing the tendency for the successively budded zooecia of one line to be ovicelled. × 30. D.40651.

FIG. 3. Ancestrula (*A*), young and adult zooecia. × 30. D.40633.

FIG. 4. Ancestrula and first ring of zooecia. × 30. D.40588.

FIG. 5. Adult zooecia and interzooecial avicularia (*a*). × 30. D.40559.

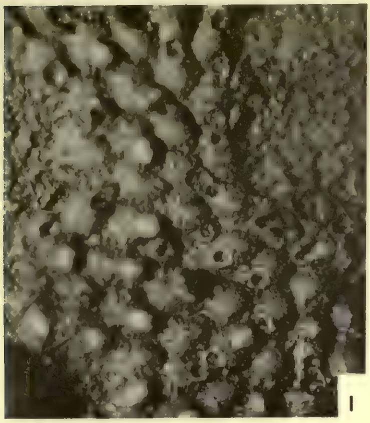
FIG. 6. Adult zooecia, showing particularly the form of the apertural bars and interzooecial avicularia (*a*). × 30. D.40579.

FIG. 7. Ancestrula and young zooecia. × 30. D.40589.

Aeolopora nebulosa Lang

FIG. 8. Adult zooecia, showing thick apertural bars. × 30. D.40661.

FIG. 9. Ancestrula (*A*) and young zooecia with thick apertural bars. Holotype. × 30. D.29061.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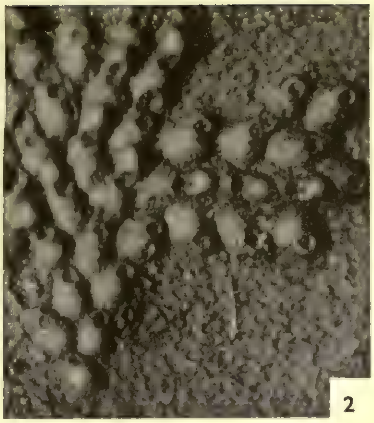
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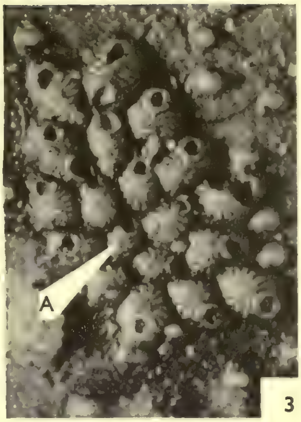

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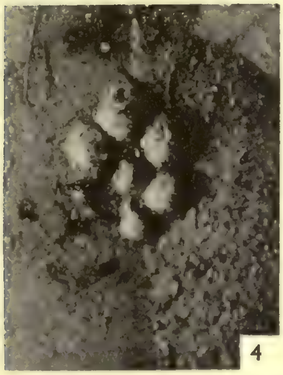
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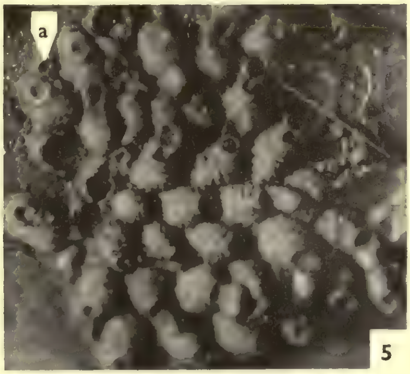

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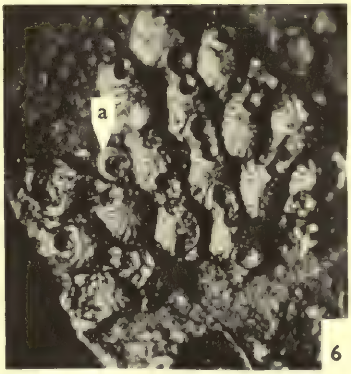

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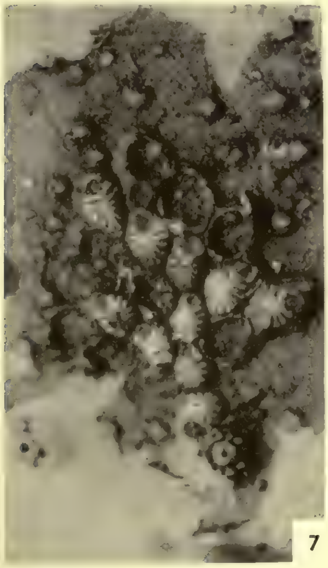
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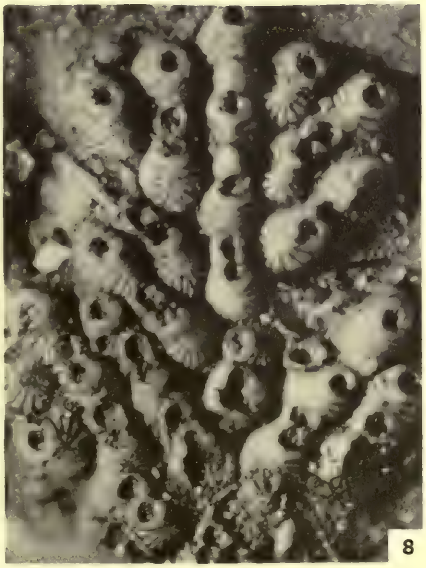
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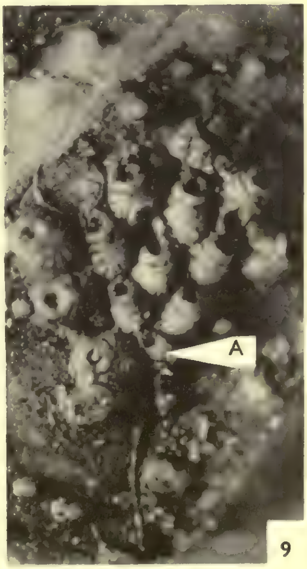


9

AEOLOPORA

PLATE 3

Lagynopora pustulosa sp. nov.

FIG. 1. Young and adult zooecia, some with ovicells, showing prominent proximal oral shield (*pos*) and boss-like pelmatidia (*p*). Holotype. ×32. D.39419.

Lagynopora horsleyensis Lang

FIG. 2. Adult ovicelled zooecia with lateral costal fusions and interzooecial avicularia (*a*). A large distal communication pore (*cp*) is visible in some zooecia. Holotype. ×20. D.28908.

FIG. 3. Group of larger, adult ovicelled zooecia. ×20. N.C.M. 247.956 (4/2).

Lagynopora saltdeanensis Lang

FIG. 4. Poorly preserved group of adult ovicelled zooecia, some with proximal oral shield (*pos*) complete. Holotype. ×20. D.28896.

Lagynopora praecursor (Lang)

FIG. 5. Adult part of the zoarium with two relatively complete ovicelled zooecia showing the enlarged proximal-lateral oral spines and large, oval, interzooecial avicularia (*a*). Holotype. ×20. D.8351.

Lagynopora birlingensis Lang

FIG. 6. Group of adult ovicelled zooecia ; proximal oral shield (*pos*). Holotype. ×20. D.28254.

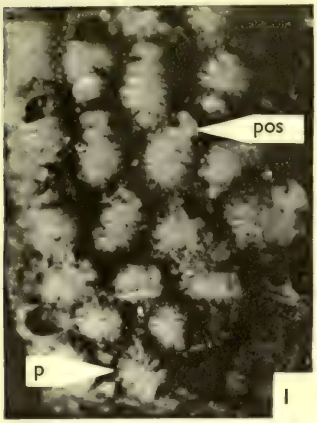
Lagynopora ampulla Lang

FIG. 7. Adult ovicelled zooecia ; proximal oral shield (*pos*). Holotype. ×20. D.28256.

FIG. 8. Ovicelled zooecia and prominent distal communication pore (*cp*). Holotype. ×20. D.28256.

Lagynopora amphora Lang

FIG. 9. Adult zooecia with damaged ovicells. Holotype. ×20. D.28255.



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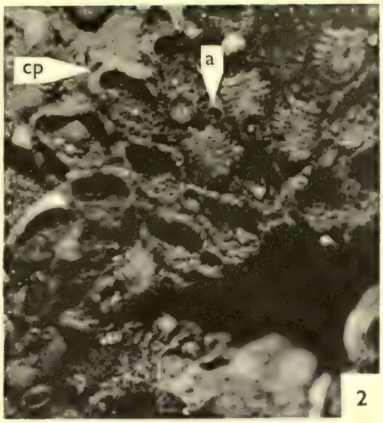

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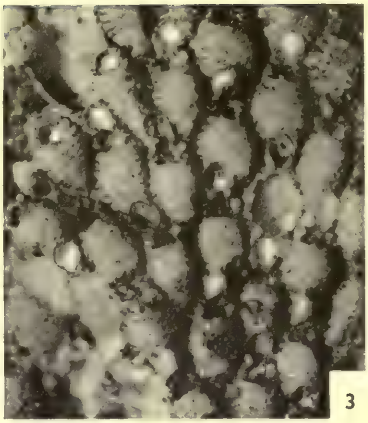

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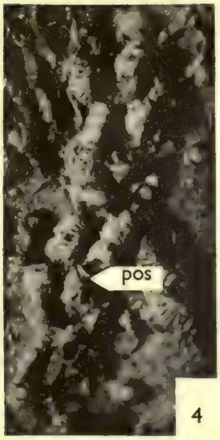

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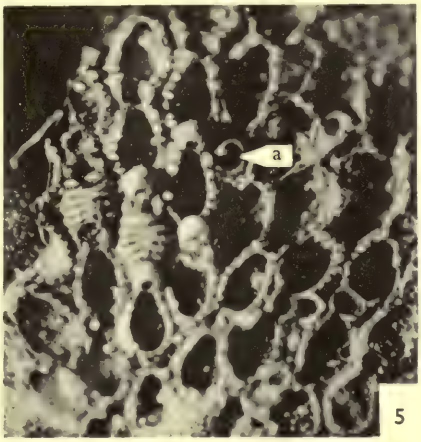

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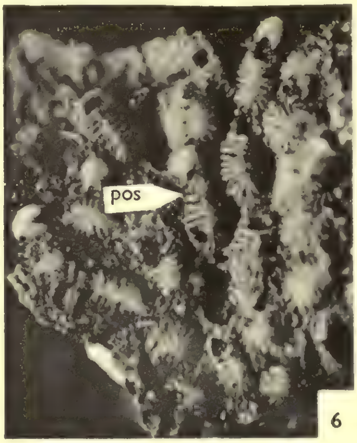

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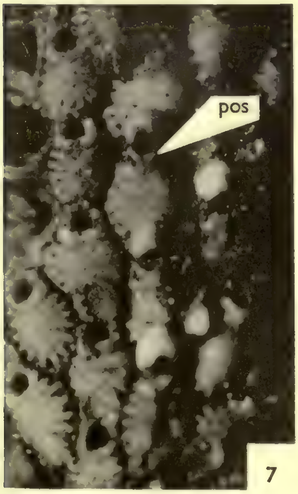

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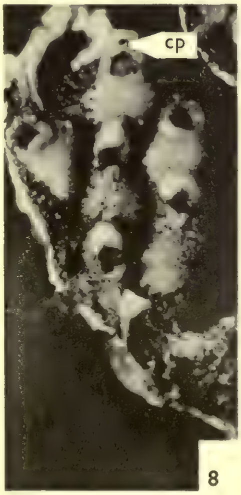

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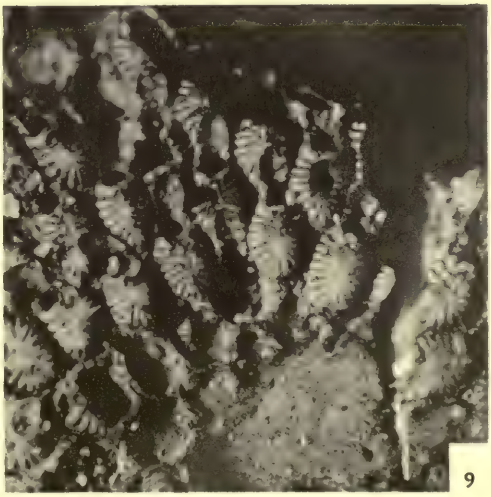


9

LAGYNOPORA

PLATE 4

Lagynopora furcifera (Brydone)

FIG. 1. Part of the extensive zoarium with well-preserved adult ovicelled zooecia and several complete proximal oral shields (*pos*). Lectotype. ×20. S.M., B.36165.

FIG. 2. Young zooecia with six oral spine bases (*os*) and an oval, interzooecial avicularium (*a*). Lectotype. ×20. S.M., B.36165.

Lagynopora ollula Lang

FIG. 3. Adult ovicelled zooecia; proximal oral shield (*pos*), oval, interzooecial avicularia (*a*). Lectotype. ×20. S.M., B.36166.

Lagynopora lagena Lang

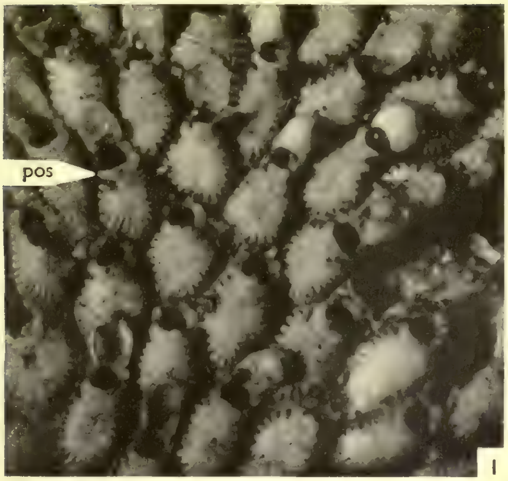
FIG. 4. Ancestrula (*A*), young and adult zooecia. Holotype. ×20. D.4042.

FIG. 5. Ovicelled adult zooecia, some with complete proximal oral shields (*pos*). Paratype. ×20. D.4028.

FIG. 6. Adult zooecia, with broken proximal oral shields, showing the form of the apertural bar (*ab*). Paratype. ×20. D.2633.

Lagynopora urceolus Lang

FIG. 7. Adult ovicelled zooecia with broken proximal oral shields, an incomplete one is marked (*pos*). Distal communication pores (*cp*) are visible at the edges of the zoarial fragment. Holotype. ×20. D.28889.



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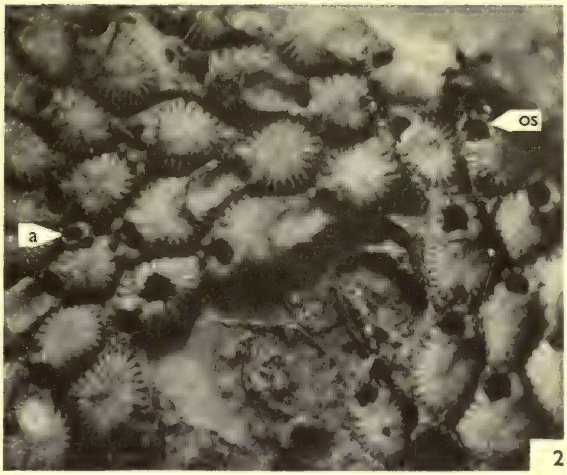

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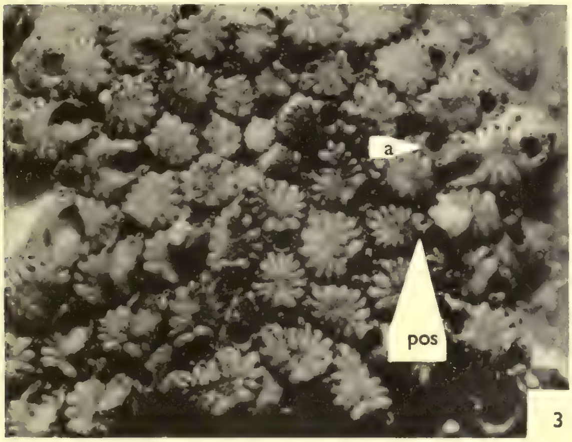

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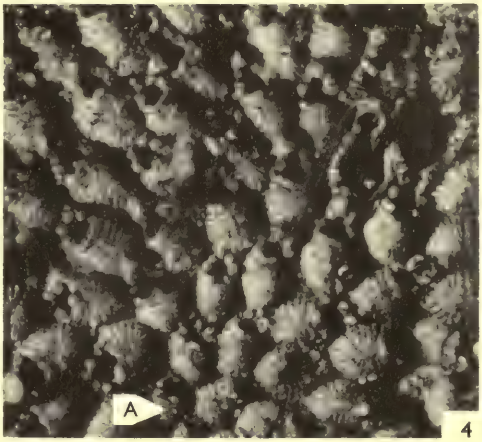

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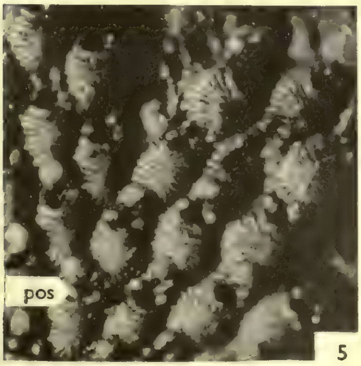

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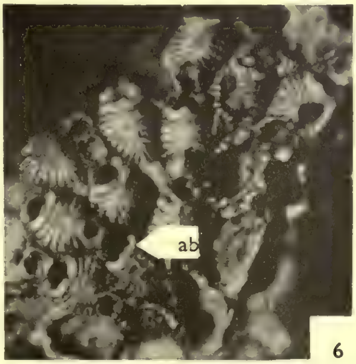

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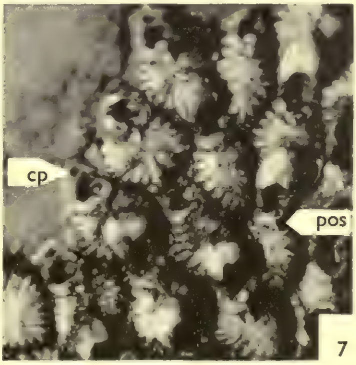

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LAGYNOPORA

PLATE 5

Lagynopora urceolus Lang

FIG. 1. Extensive zoarium with adult ovicelled zooecia and prominent interzooecial avicularia (*a*). ×20. D.41067.

Lagynopora vasculum Lang

FIG. 2. Obscured ancestrula (*A*), young, and adult ovicelled zooecia, some with well-preserved proximal oral shields (*pos*) and interzooecial avicularia (*a*). Lectotype. ×20. S.M., B.36164.

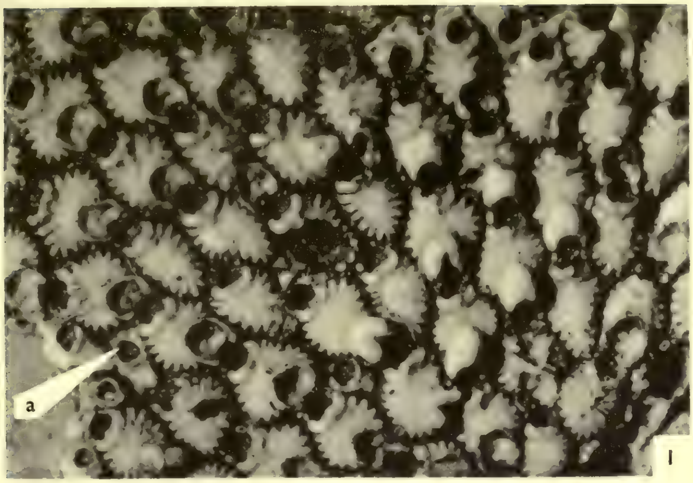
Hexacanthopora sexspinosa Lang

FIG. 3. Well-preserved zoarium, with ancestrula (*A*) and broken, worn ovicells. The broken zooecia near the edge of the zoarial fragment reveal distal and lateral pore chambers (*pc*). Holotype. ×20. D.21205.

FIG. 4. Distal (*dcp*) and lateral (*lcp*) communication pores are visible. Paratype. ×20. D.21206.

FIG. 5. Poorly preserved adult zooecia; the circum-ancestrular area destroyed. Large avicularia present (*a*). Holotype of *H. brightonensis* Lang. ×20. D.28890.

FIG. 6. Adult ovicelled zooecia with median processes (*mp*) on the apertural bars and large avicularia (*a*). Holotype of *H. kintburiensis* Lang. ×20. D.21204.



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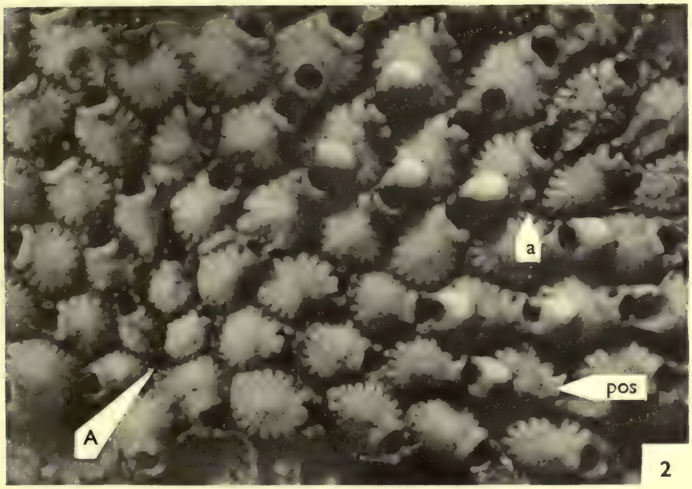

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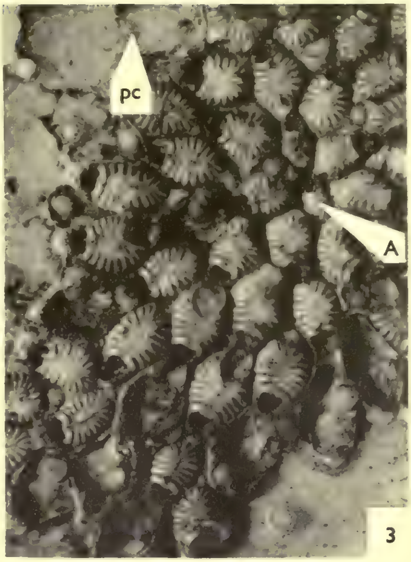

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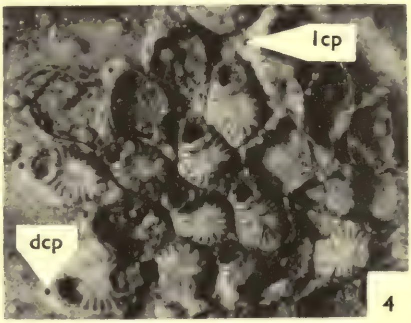

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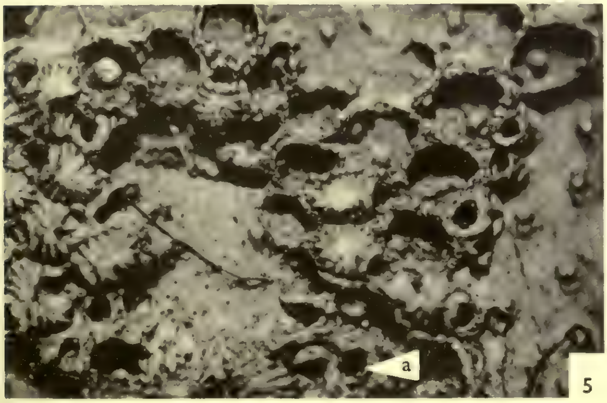

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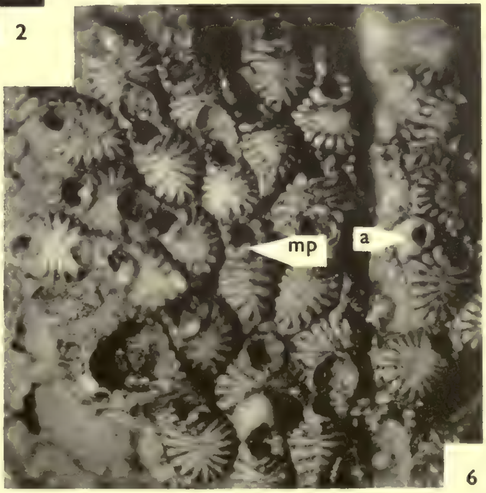

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LAGYNOPORA, HEXACANTHOPORA

PLATE 6

Leptocheilopora magna Lang

FIG. 1. Ancestrula and young zooecia; pelmatidia (*p*) visible on the costae of some zooecia. Holotype. ×20. D.19623.

FIG. 2. Adult zooecia, some with broken ovicells. ×20. D.38919.

FIG. 3. Adult zooecia, some with broken ovicells (*o*). ×20. D.38918.

FIG. 4. Ancestrula and young zooecia. ×20. D.39424.

FIG. 5. Adult zooecia with three complete ovicells. The minute oral spine bases (*os*) are visible and distal and lateral communication pores are exposed near the edge of the zoarial fragment. ×20. D.39425.

FIG. 6. Ancestrula (*A*) and young zooecia. The apertural bar of the zooecium on the left is particularly well preserved showing the small median ridge which is sometimes present. ×20. D.39426.

FIG. 7. ? *Leptocheilopora magna* Lang. Copy of part of a photograph in the British Museum (Natural History) of the holotype of *L. longuessensis* Lang.

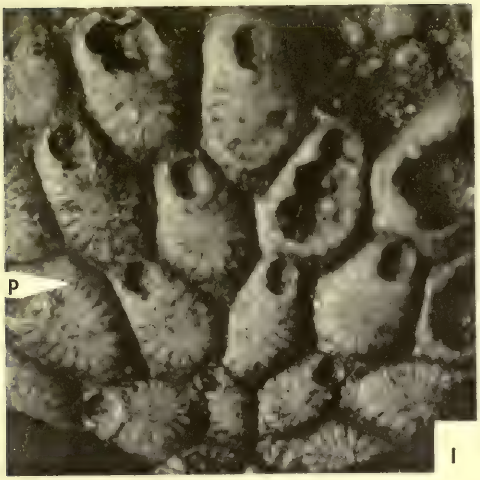
Leptocheilopora tenuilabrosa Lang

FIG. 8. Adult zooecia with broken, costate ovicells (*o*). Holotype. ×20. D.28892.

FIG. 9. Adult zooecia. Holotype of *L. gasteri* Lang. ×20. D.29901.

FIG. 10. Two adult zooecia, one with complete costate ovicell. Holotype of *L. gasteri* Lang. ×20. D.29901.

FIG. 11. Adult zooecia and broken costate ovicells (*o*). Paratype of *L. tenuilabrosa* Lang. ×20. D.21210.



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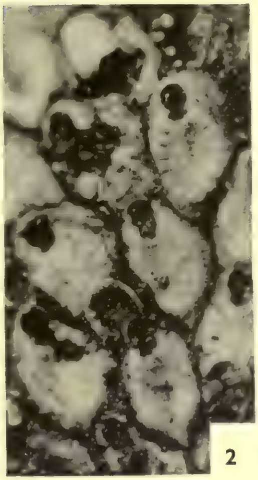

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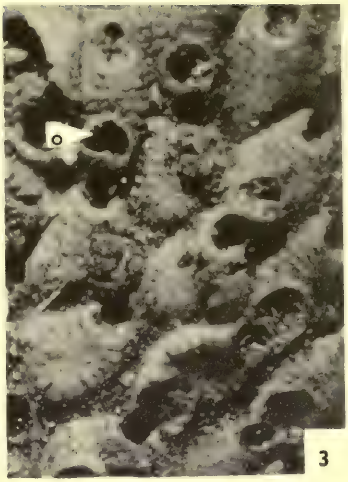

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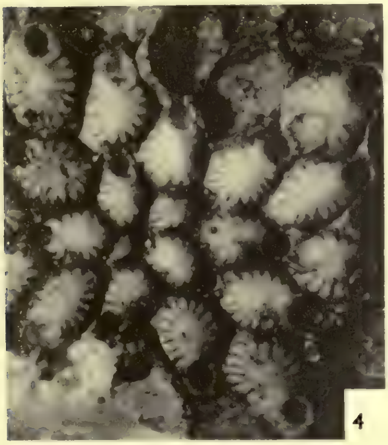

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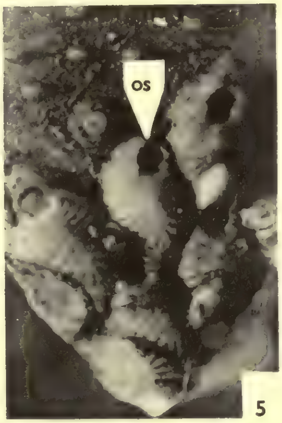

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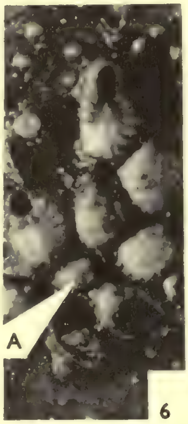

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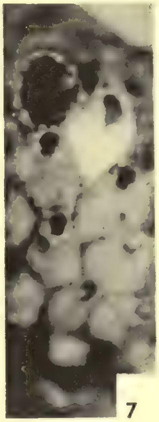

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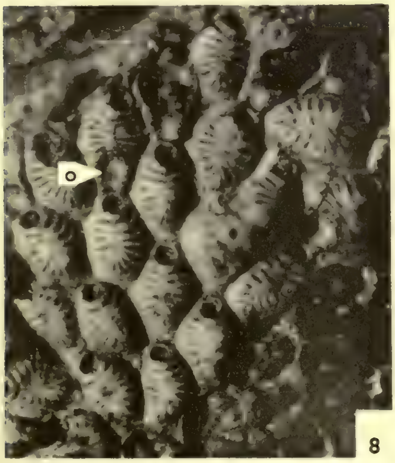

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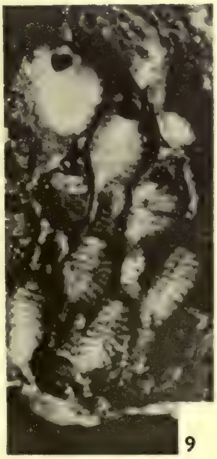

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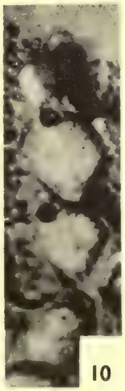

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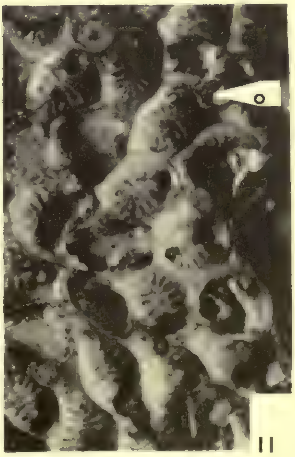

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LEPTOCHEILOPORA

PLATE 7

Leptocheilopora tenuilabrosa Lang

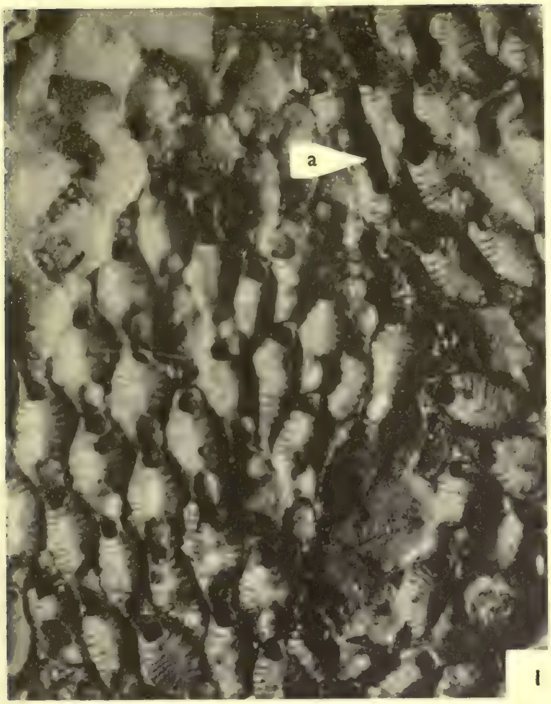
FIG. 1. Adult ovicelled zooecia with large, spatulate avicularium with costate frontal shield (*a*). ×20. Figured Brydone (1917, pl. 3, fig. 7) as *Cribrilina tumuliformis*. S.M., B.36338.

FIG. 2. Adult zooecia and large, vicarious, spatulate avicularium with costate frontal shield and minute apertural spine bases (*a*). ×20. Figured Brydone (1917, pl. 3, fig. 8) as *Cribrilina tumuliformis*. S.M., B.36339.

Leptocheilopora filliozati (Brydone)

FIG. 3. Adult zooecia, some ovicelled; distal communication pores (*dcp*) visible in some zooecia. Lectotype. ×20. S.M., B.36167.

FIG. 4. Adult zooecia with typical median ridges on each frontal shield. Holotype of *L. arcuata* Lang. ×20. D.28294.



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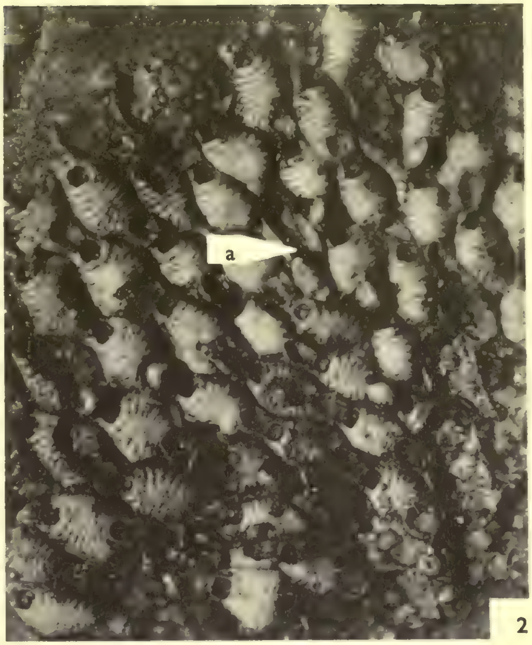

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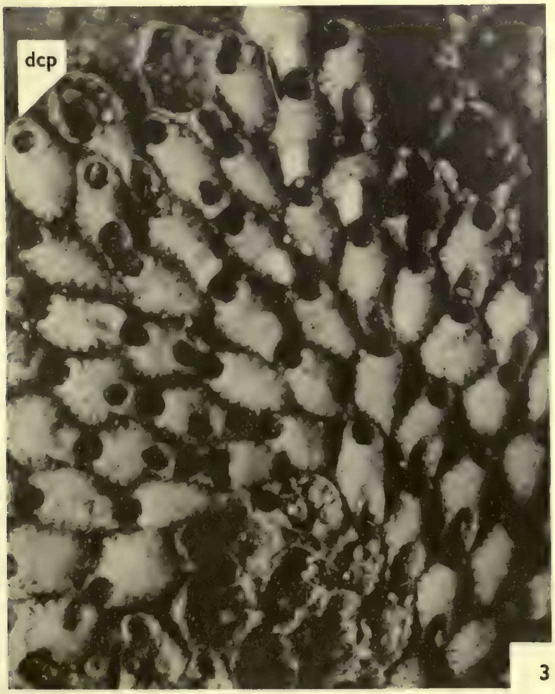

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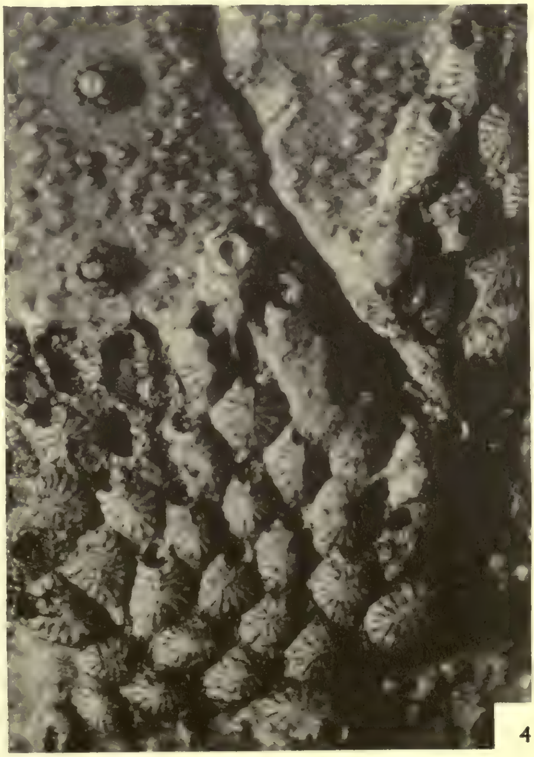

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LEPTOCHEILOPORA

PLATE 8

Leptocheilopora filliozati (Brydone)

FIG. 1. Well-preserved group of adult zooecia, one exceptionally long with 35 costae. × 20. D.40940.

FIG. 2. Group of adult zooecia. × 20. D.39427.

FIG. 3. Ancestrula (*A*), young and adult zooecia with marked median ridge on the frontal shield. × 20. Paratype of *L. arcuata* Lang. D.4279.

FIG. 4. The only specimen in the British Museum (Natural History) labelled by Lang "*Leptocheilopora filliozati* (Brydone)". Two adult zooecia, the most distal with a distal communication pore, and two small zooecia to the right. × 20. D.29900.

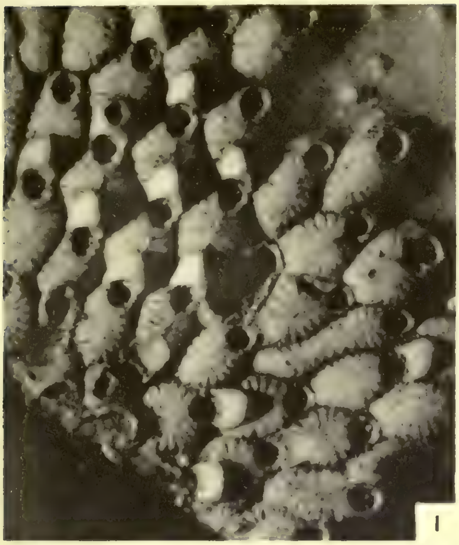
FIG. 5. Very young zooecia with ?ancestrula. Paratype of *L. arcuata* Lang. × 20. D.28895.

FIG. 6. Adult zooecia, some with slightly damaged ovicells. Paratype of *L. arcuata* Lang. × 20. D.28893.

FIG. 7. Adult ovicelled zooecia with marked median ridges on frontal shields and very young zooecia (*Y*). × 20. S.M., B.36168.

FIG. 8. Ancestrula (*A*), young and adult zooecia with well-displayed distal communication pores. × 20. D.39430.

FIG. 9. Edge of a damaged zoarial fragment with adult zooecia with distinct distal and lateral communication pores. × 20. D.39429.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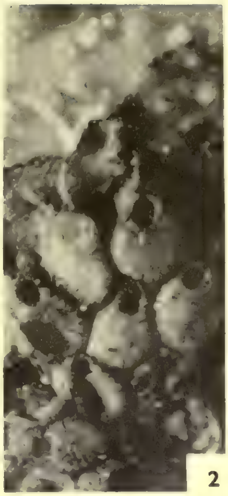
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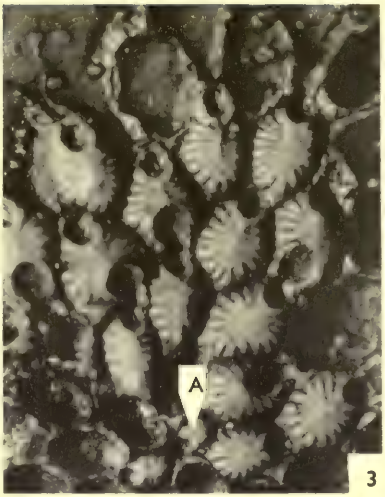

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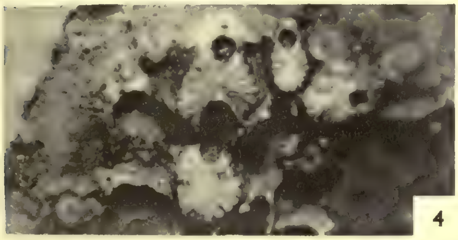
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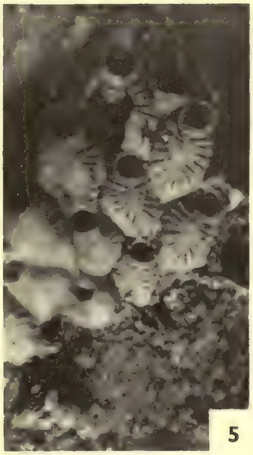
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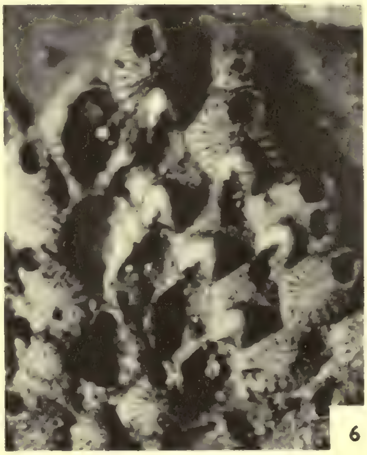
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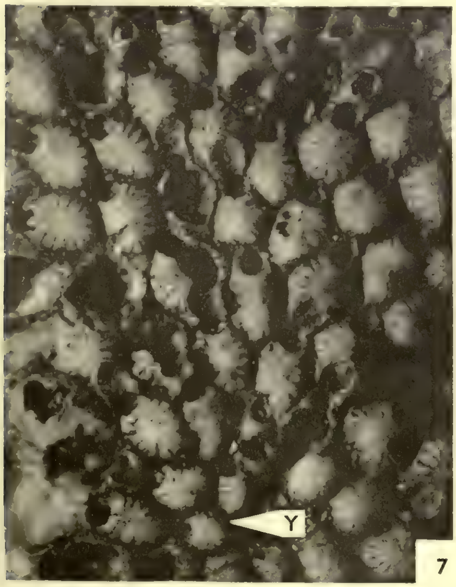

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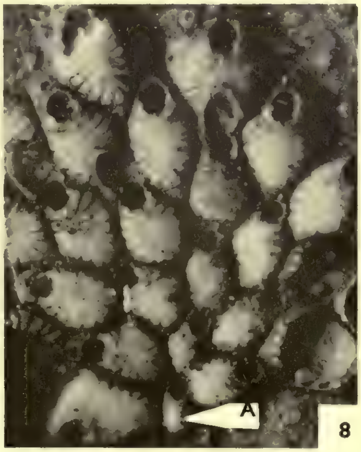

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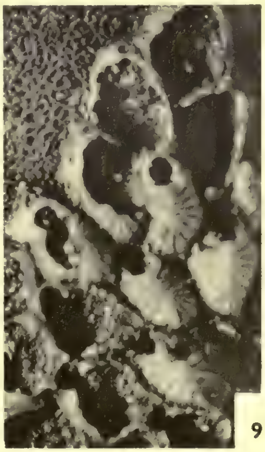
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LEPTOCHEILOPORA

PLATE 9

Leptocheilopora vulnerata (Brydone)

FIG. 1. Young and adult zooecia, those at the top with visible pelmata (*p*). Lectotype. ×20. S.M., B.36271.

FIG. 2. Extensive zoarium of young and adult, ovicelled zooecia. ×20. S.M., B.36272.

Pelmatopora calceata Lang

FIG. 3. Adult zooecia with well-exposed gymnocyst, prominent, large pelmata and small, round, sporadic avicularia. Holotype. ×20. D.4032.

Pelmatopora crepidaria Lang

Fig. 4. Adult zooecia with tubular avicularia (*a*). One zooecium with ? the remains of a broken calcareous lamina in the orifice (*cl*). Holotype. ×20. D.21200.

Pelmatopora solearis Lang

FIG. 5. Group of adult zooecia. Holotype. ×20. D.21211.

FIG. 6. Group of young zooecia with well-exposed gymnocyst (*g*). Holotype. ×20. D.21211.

Pelmatopora chrysalis (d'Orbigny)

FIG. 7. Group of adult zooecia. Copy of a photograph in the British Museum (Natural History) of the middle specimen of three on a slide labelled " *Escharipora striata* d'Orbigny, Coniacian, Villedieu ". F. Canu Collection, Paris.

Pelmatopora gasteri Lang

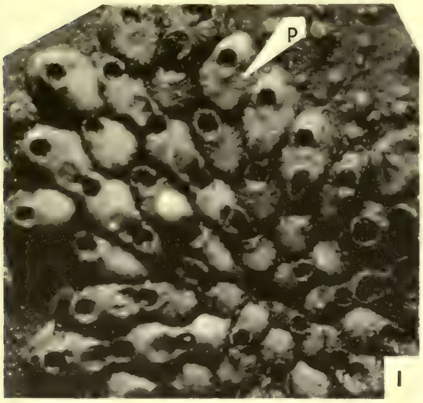
FIG. 8. Adult zooecia with small orifices with distinct proximal-lateral constrictions. Holotype. ×20. D.28274.

Pelmatopora larva Lang

FIG. 9. Long adult zooecia with paired, distally pointed and directed avicularia (*a*). Holotype. ×20. D.28440.

Pelmatopora striata (d'Orbigny)

FIG. 10. Group of adult zooecia. Copy of a photograph in the British Museum (Natural History) of one of the outer specimens of three on a slide labelled " *Escharipora striata* d'Orbigny, Coniacian, Villedieu ". F. Canu Collection, Paris.



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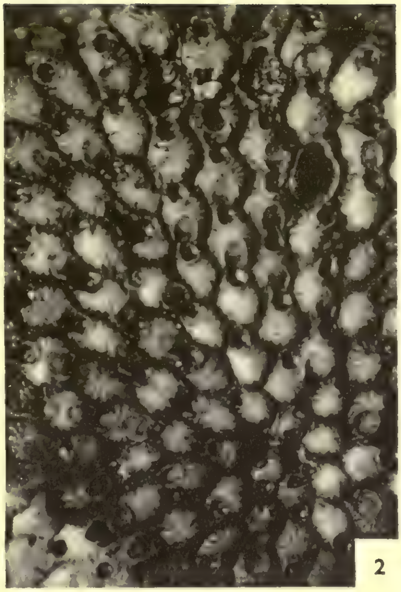

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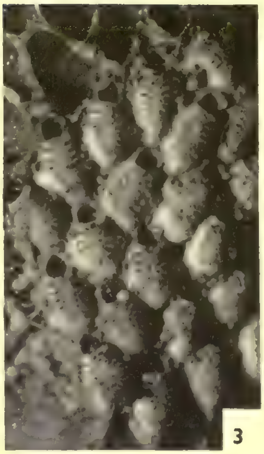

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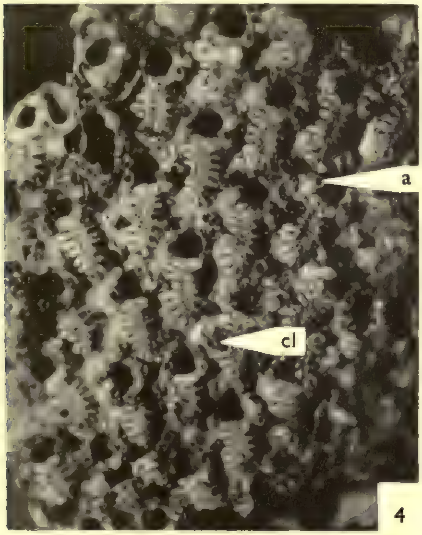

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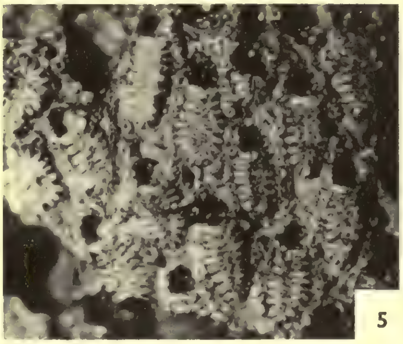

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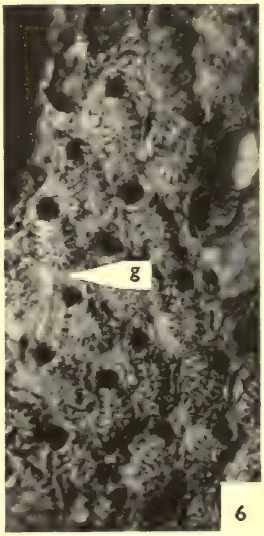

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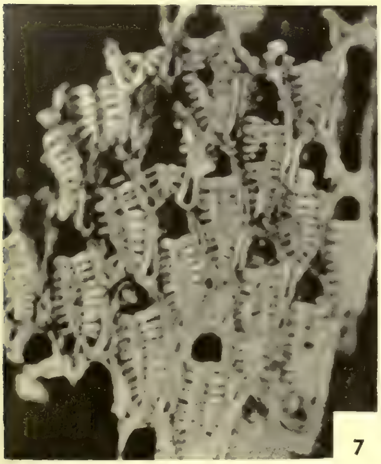

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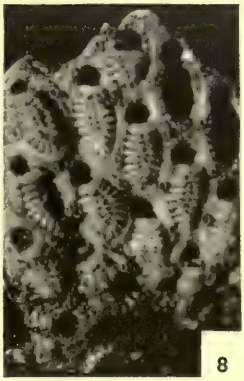

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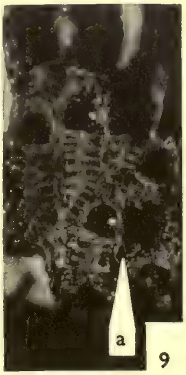

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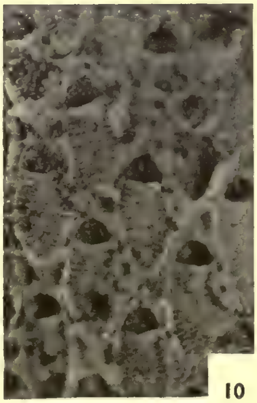

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LEPTOCHEILOPORA, PELMATOPORA

PLATE 10

Pelmatopora fragilis (d'Orbigny)

FIG. 1. Copy of a photograph in the British Museum (Natural History) of one of three specimens on a slide labelled " *Cribrilina* [*Semiescharipora*] *fragilis* d'Orbigny ". Senonian, Emscherian, Fécamp, Seine Inférieure, France. F. Canu Collection, Paris.

FIG. 2. Adult zooecia with commonly paired avicularia. Holotype of *Pelmatopora pauciclavia* Lang. ×20. D.28273.

Pelmatopora d'orbignyi Lang

FIG. 3. Group of adult zooecia with prominent, paired avicularia (*a*) and abundant interzooecial secondary tissue with deep lacunae (*l*). Holotype. ×20. D.28453.

Pelmatopora quadrata Lang

FIG. 4. Adult zooecia with commonly paired avicularia (*a*) and well immersed ovicells (*o*). Holotype. ×20. D.28271.

FIG. 5. Group of adult zooecia. Copy of a photograph in the British Museum (Natural History) of a specimen mounted nearest to the label on a slide labelled " *Cribrilina* [*Semiescharipora*] *fragilis* d'Orbigny ". Senonian, Emscherian, Fécamp, Seine Inférieure, France. F. Canu Collection, Paris. Lang (1922 : 273) made the specimen the holotype of *Pelmatopora filliozati* Lang.

Pelmatopora fecampensis Lang

FIG. 6. Adult zooecia with paired, distally pointed and directed avicularia (*a*). The orifice may be closed by a thin, calcareous lamina (*cl*) as in the zooecium on the left. Holotype. ×20. D.28473.

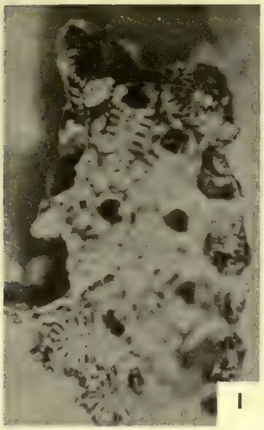
Pelmatopora pero Lang

FIG. 7. Adult zooecia with prominent, distally pointed and directed avicularia (*a*). Holotype. ×20. D.23405.

Pelmatopora suffulta (Brydone)

FIG. 8. Edge of zoarial fragment with pointed, distally directed avicularia and adult ovicelled zooecia. Lectotype of *P. repleta* (Brydone). ×20. S.M., B.36263. Figured Brydone (1913, pl. 14, fig. 5) as *Cribrilina suffulta*.

FIG. 9. Adult zooecia with widely exposed gymnocysts (*g*). Lectotype of *Pelmatopora suffulta* (Brydone). ×20. S.M., B.36262. Figured Brydone (1913, pl. 14, fig. 4) as *Cribrilina suffulta* and chosen as lectotype of *Pelmatopora suffulta* (Brydone) by Lang (1922 : 277).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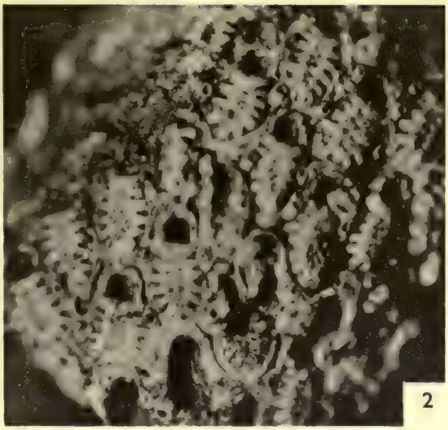
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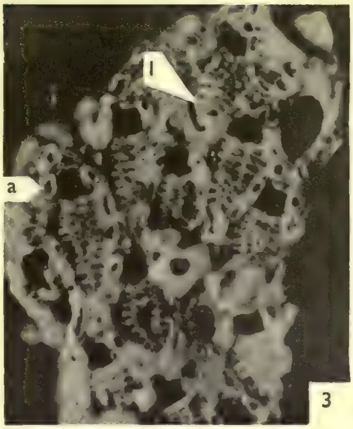

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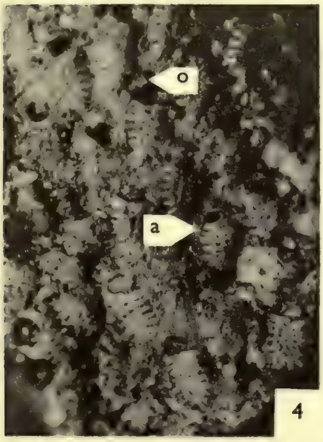

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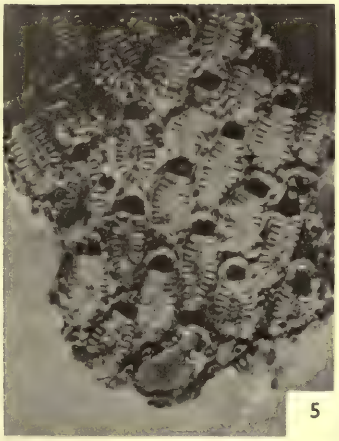
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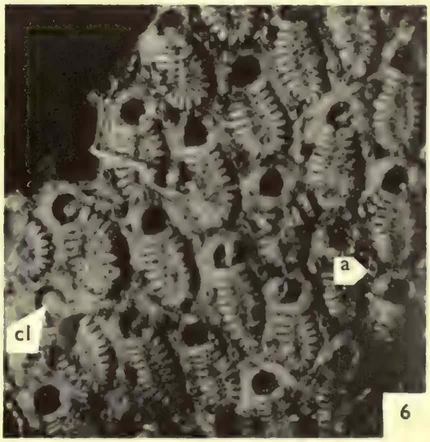

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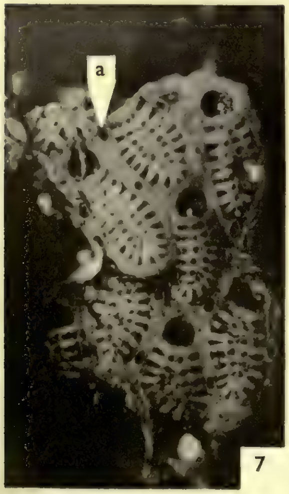

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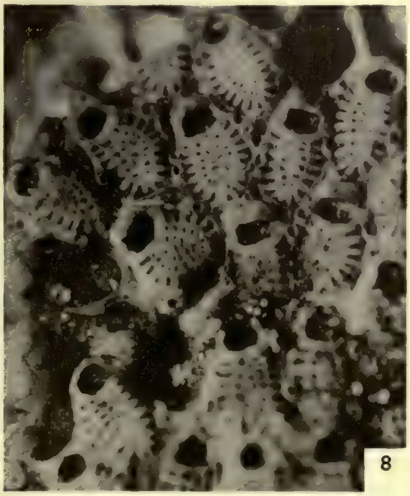
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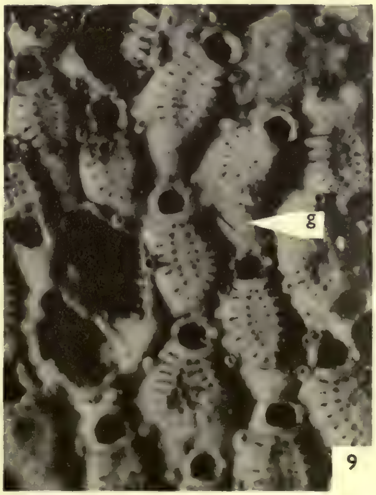

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PELMATOPORA

PLATE 11

Pelmatopora suffulta (Brydone)

Fig. 1. Adult zooecia with pointed avicularia (*a*). Lectotype of *P. repleta* (Brydone). ×20. S.M., B.36263.

Pelmatopora simplex Lang

Fig. 2. Adult zooecia with deep interzooecial lacunae (*l*). Holotype. ×20. D.28281.

Fig. 3. Young zooecia. Holotype. ×20. D.28281.

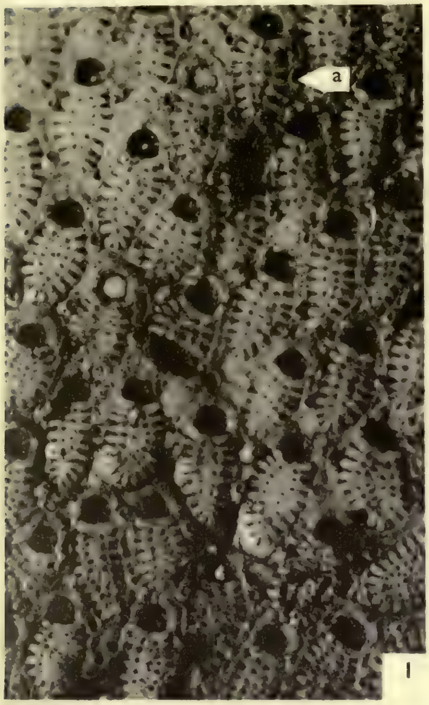
Pelmatopora plantaris Lang

Fig. 4. Adult zooecia, with sharply defined interzooecial lacunae (*l*), and young zooecia (*Y*). Holotype. ×20. D.19620.

Pelmatopora quadrivolucris Lang

Fig. 5. Adult zooecia, each with two pairs of enlarged oral spines. Holotype of *Cribrilina galanthis* Brydone. ×20. S.M., B.36261.

Fig. 6. Adult zooecia, each with two pairs of enlarged oral spines. Holotype of *Pelmatopora quadrivolucris* Lang. ×20. D.28907.



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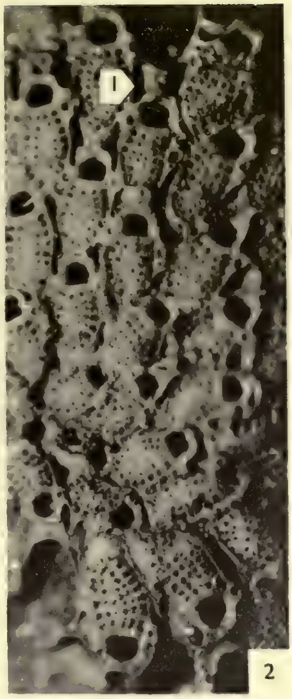

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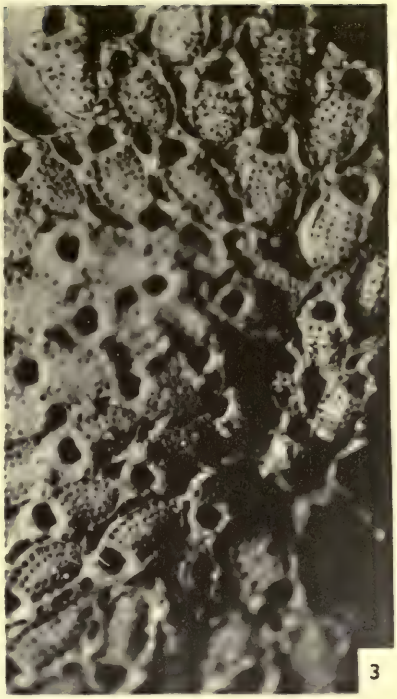
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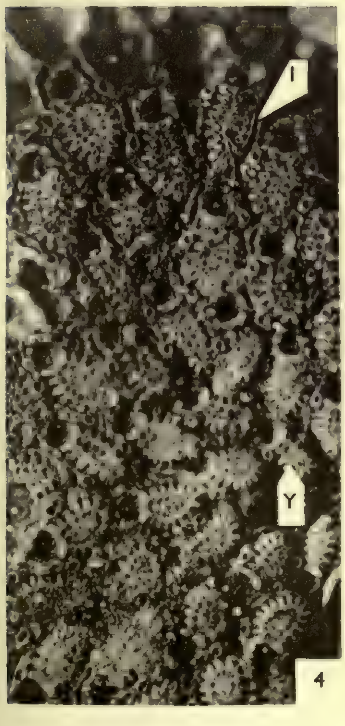

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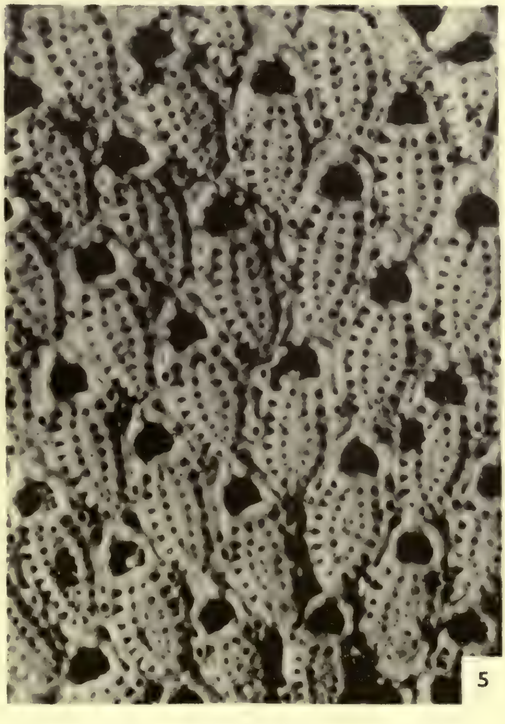
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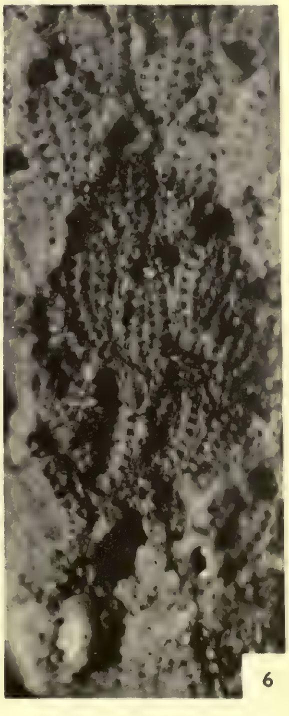
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PELMATOPORA

PLATE 12

Pelmatopora quadrivolucris Lang

FIG. 1. Adult zooecia, each with two pairs of enlarged oral spines. ×20. S.M., B.36363.

Pelmatopora marsupitorum Lang

FIG. 2. Adult zooecia, showing enlarged, peg-like, distal oral spines (*d*) and secondary thickening (*st*) obscuring the lateral oral spines. Holotype. ×20. D.28867.

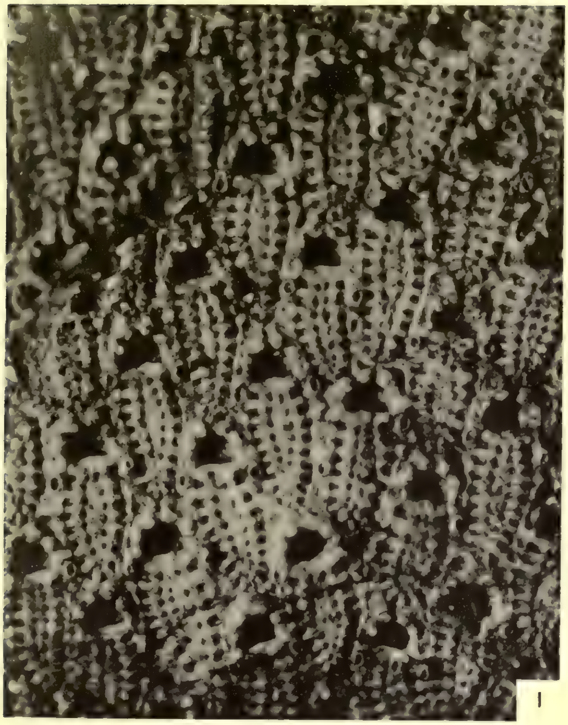
FIG. 5. Adult zooecia, one with an ovicell (*o*). Holotype of *P. roedeanensis* Lang. × 20. D.28868.

Pelmatopora brydonei Lang

FIG. 3. Adult zooecia, showing enlarged distal oral spines and visible, unmodified, proximal-lateral oral spine bases. Holotype. ×20. D.23396.

Pelmatopora coryli (Lang)

FIG. 4. Adult zooecia with enlarged distal oral spines. Holotype. ×20. D.28998.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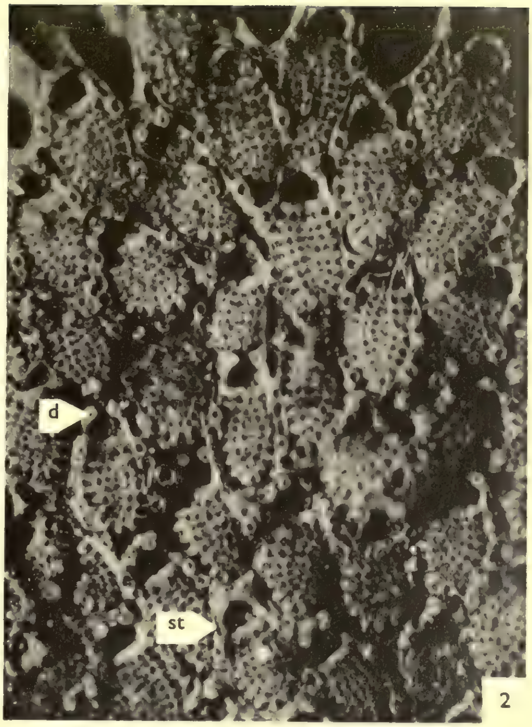

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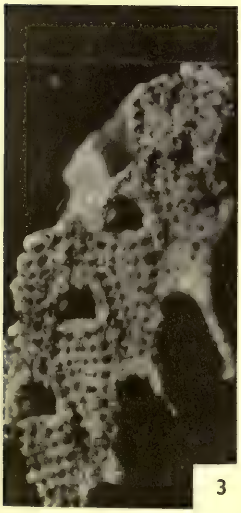
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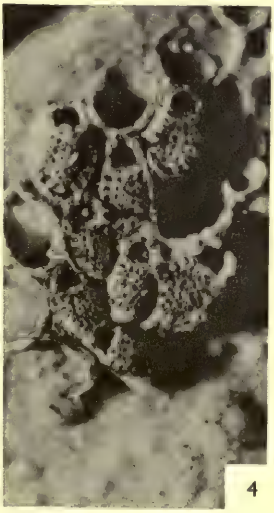
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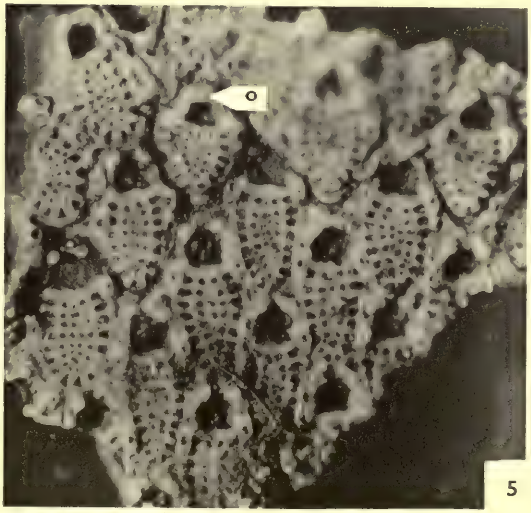

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PELMATOPORA

PLATE 13

Pelmatopora gregoryi (Brydone)

FIG. 1. Adult zooecia with plentiful interzooecial secondary tissue. The orifices of ovicelled zooecia (*o*) are oblong. Lectotype. × 20. S.M., B.36120.

FIG. 2. Adult zooecia, some ovicelled (*o*). Holotype of *P. bidens* Lang. × 20. D.28934.

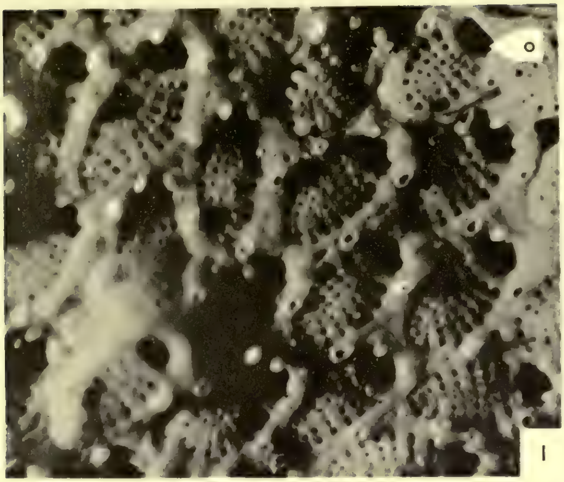
FIG. 3. Adult zooecia with abundant interzooecial secondary tissue. Holotype of *P. collium* Lang. × 20. D.28824.

FIG. 4. Adult zooecia. Holotype of *P. lancingensis* Lang. × 20. D.28947.

FIG. 5. Probably a young zooecium. Holotype of *P. gyrinoides* Lang. × 20. D.28270.

FIG. 6. Adult zooecia. Holotype of *P. saltdeanensis* Lang. × 20. D.28842.

FIG. 7. Adult zooecia. Holotype of *P. ranunculoides* Lang. × 20. D.28856.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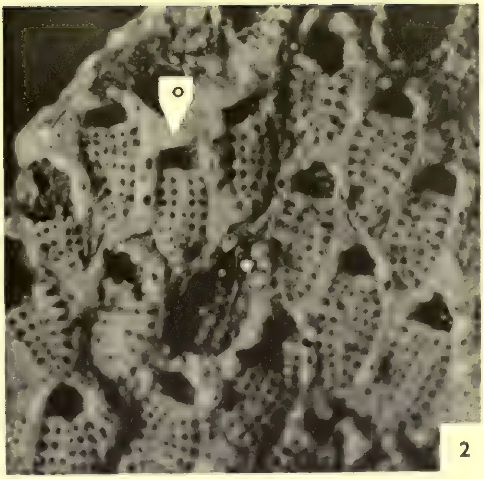
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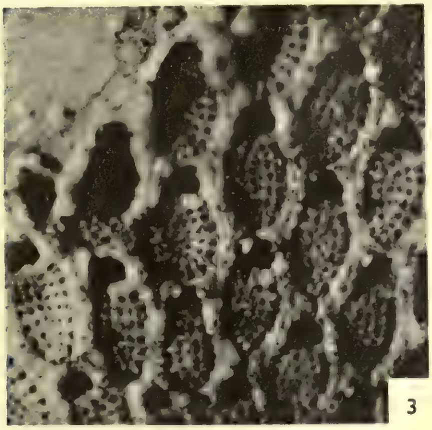
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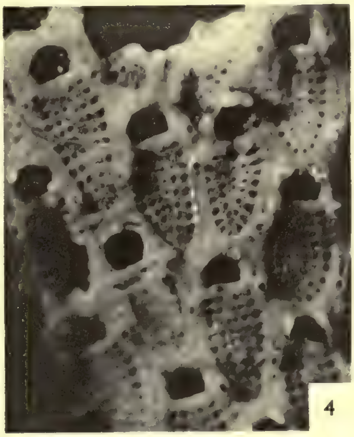
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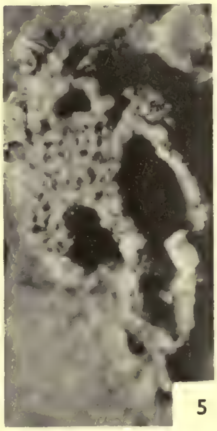
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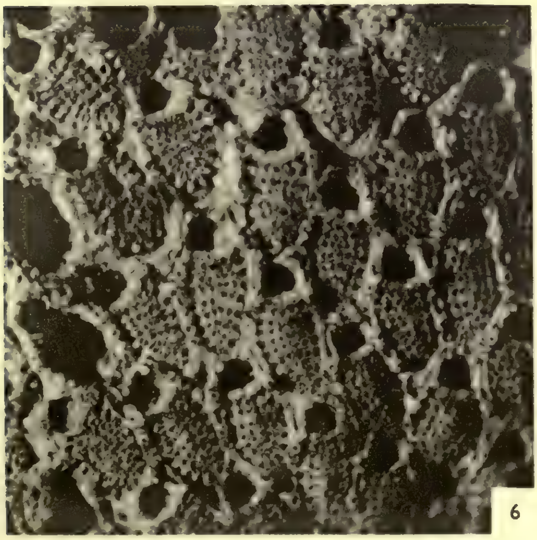
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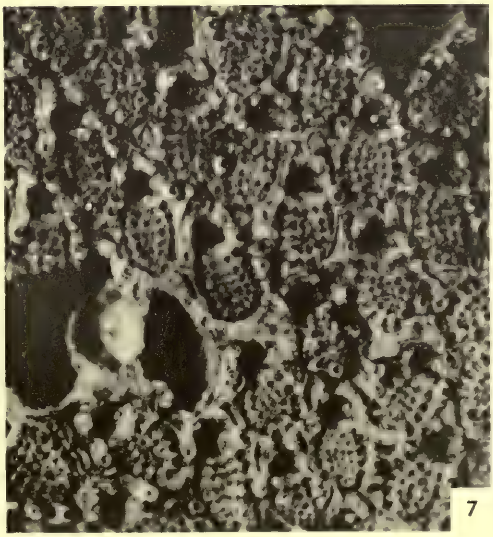
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PELMATOPORA

PLATE 14

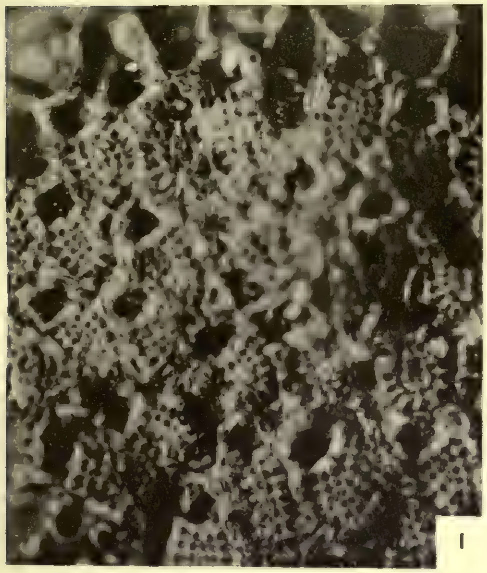
Pelmatopora gregoryi (Brydone)

FIG. 1. Adult zooecia. Holotype of *P. lacuum* Lang. × 20. D.28862.
FIG. 2. Adult zooecia. Paratype of *P. bidens* Lang. × 20. D.28828.
FIG. 3. Adult zooecia. × 20. D.39301.
FIG. 4. Adult zooecia. Holotype of *P. promontoriorum* Lang. × 20. D.28930.

Pelmatopora somptingensis Lang

FIG. 5. Adult zooecia, showing the great variation of length which may occur in the same part of a single zoarium. Very long and very short zooecia are adjacent. × 20. D.39333.

FIG. 6. Adult zooecia, showing very prominent, laterally flattened and distally expanded distal oral spines. Holotype. × 20. D.28762.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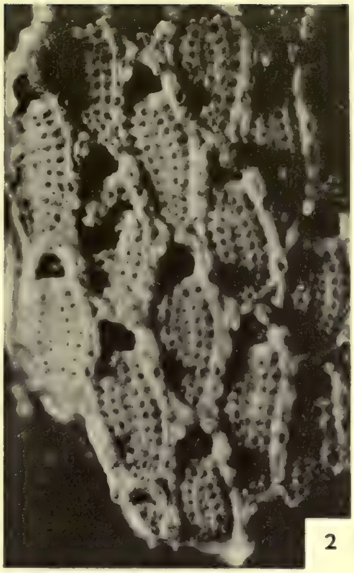
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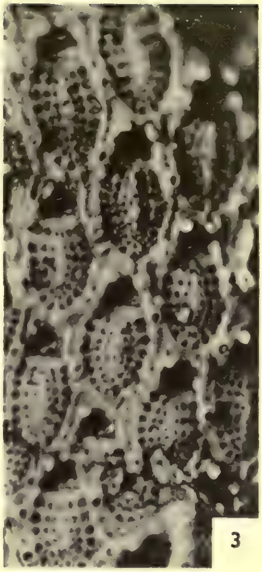
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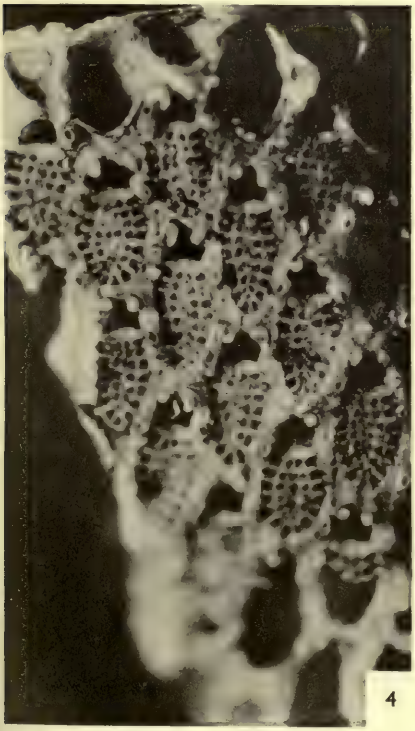
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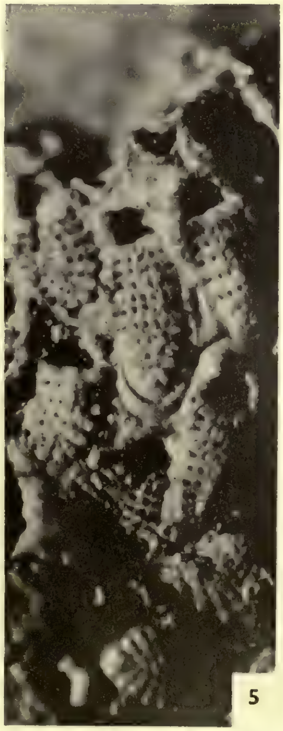
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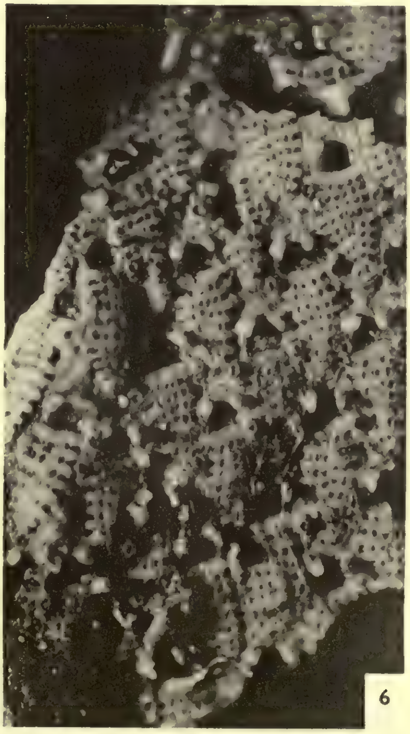
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PELMATOPORA

PLATE 15

Pelmatopora somptingensis Lang

FIG. 1. Adult zooecia. Holotype of *P. danktonensis* Lang. ×20. D.23963.

FIG. 2. Adult zooecia, some ovicelled (*o*) producing a prominent distal oral shield. ×20. D.39343.

FIG. 4. Dorsal surface of zoarium. ×20. D.39358.

Pelmatopora palmata Lang

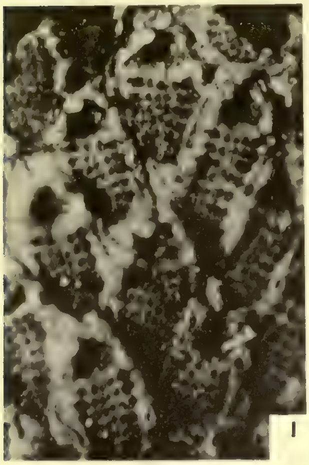
FIG. 3. Adult zooecia. Holotype of *P. damicornis* Lang. ×20. D.20204.

FIG. 5. Adult zooecia. Holotype of *P. damicornis* Lang. ×20. D.20204.

FIG. 6. Adult zooecia, with very prominent, bilobed, enlarged distal oral spines. Holotype of *P. palmata* Lang. ×20. D.8010.

Pelmatopora sp.

FIG. 7. Specimen from the Senonian, zone of *Belemnitella mucronata*. Isle of Wight. ×20. D.39330.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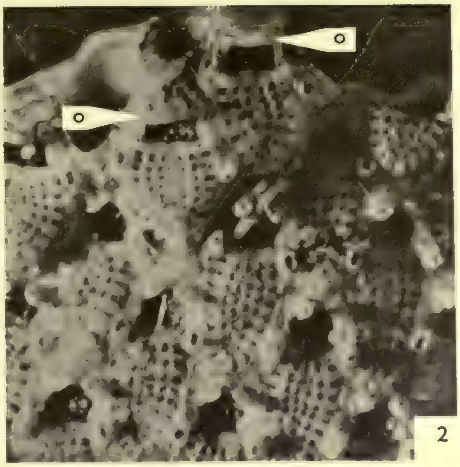
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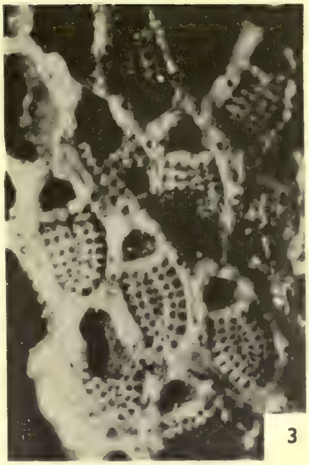
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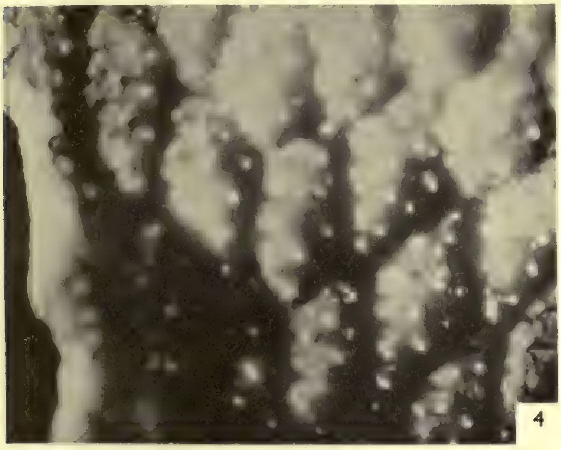
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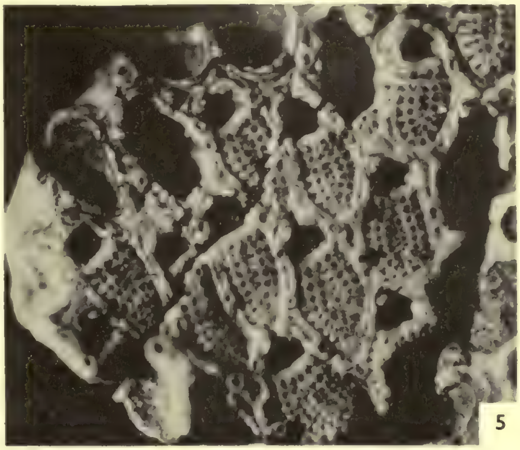
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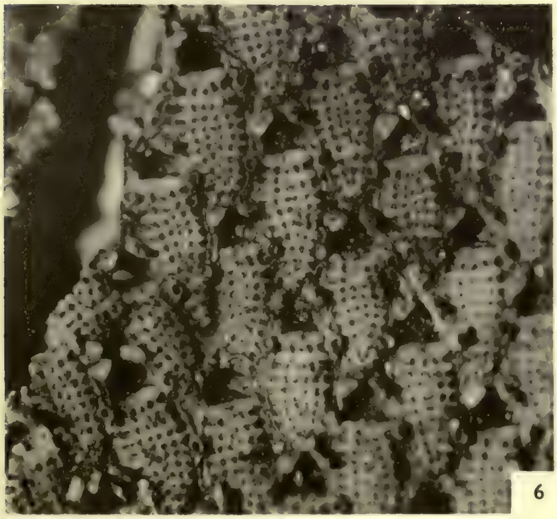
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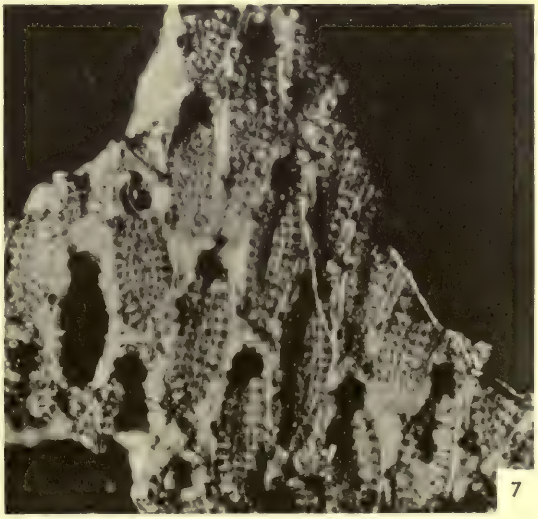
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PELMATOPORA

PLATE 16

Castanopora armata sp. nov.

FIG. 1. Adult zooecia and avicularia of types *a*, *b* and *c*. Holotype. ×20. D.31717.

Castanopora retrorsa Lang

FIG. 2. Adult zooecia, some ovicelled, with numerous interzooecial avicularia (*a*). Holotype. ×20. D.21170.

Castanopora castanea Lang

FIG. 3. Well-preserved adult zooecia with paired, distally pointed and directed avicularia (*a*). The very wide zooecium (*z*) results from the coalescence of the buds of two adjacent rows of zooecia. Holotype. ×20. D.16654.

FIG. 4. Adult zooecia with paired, distally pointed and directed avicularia. Holotype of *C. juglans* Lang. ×20. D.15608.

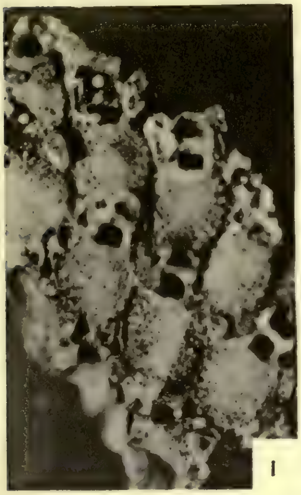
FIG. 5. Adult zooecia with paired, distally pointed and directed avicularia (*a*). The zooecium marked (*R*) has been damaged and completely regenerated. Holotype of *C. nucifera* Lang. ×20. D.15600.

Castanopora dibleyi (Brydone)

FIG. 6. Adult zooecia, some with broken ovicells (*o*), and paired, distally pointed and directed avicularia (*a*). Lectotype. ×20. S.M., B.36115.

FIG. 7. Younger part of the zoarium. Lectotype. ×20. S.M., B.36115.

FIG. 8. Adult zooecia, some with undamaged ovicells. ×20. S.M., B.36267.



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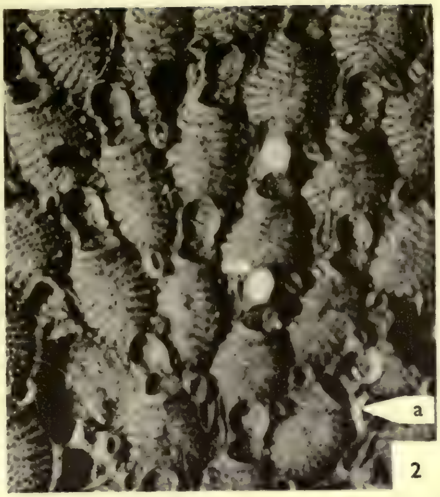

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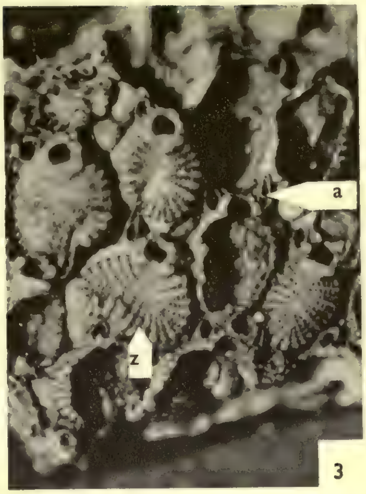

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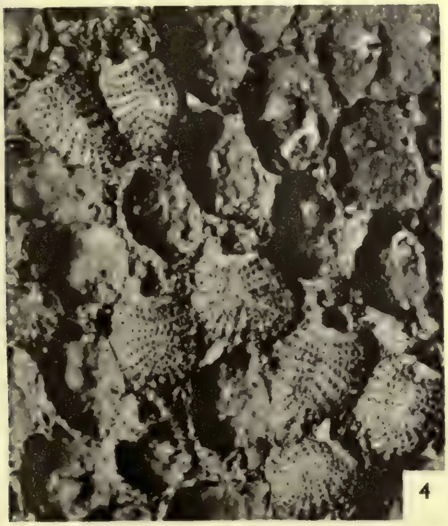

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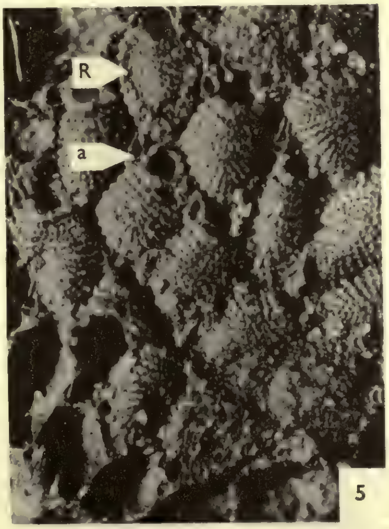

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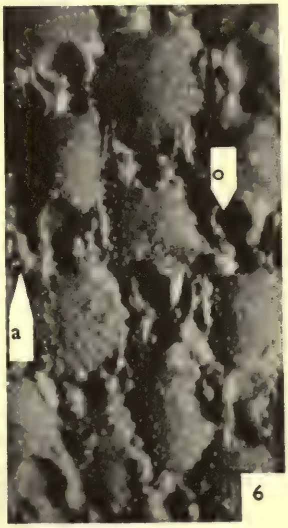

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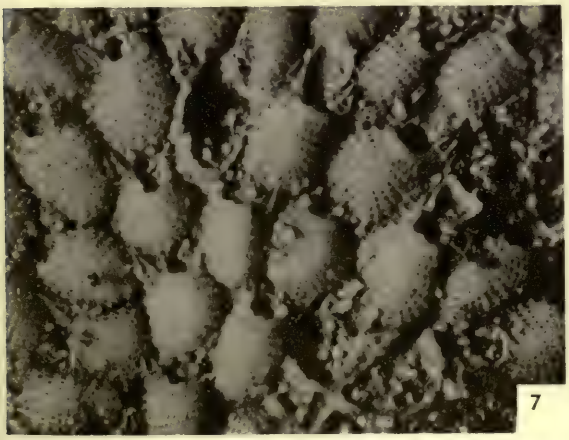

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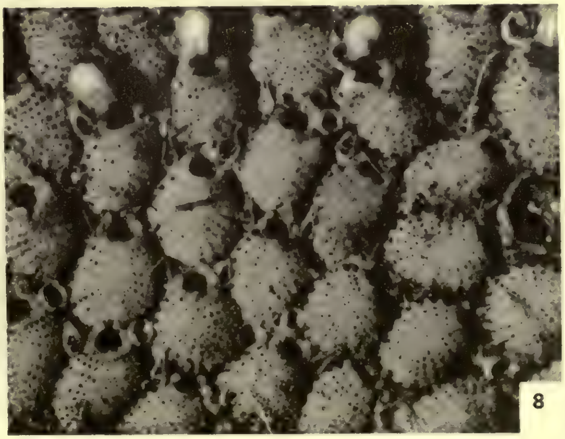

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CASTANOPORA

PLATE 17

Castanopora dibleyi (Brydone)

Fig. 1. Ancestrula, young and earlier adult zooecia. Very long avicularia (*a*) occur in the adult stages. ×20. S.M., B.36267.

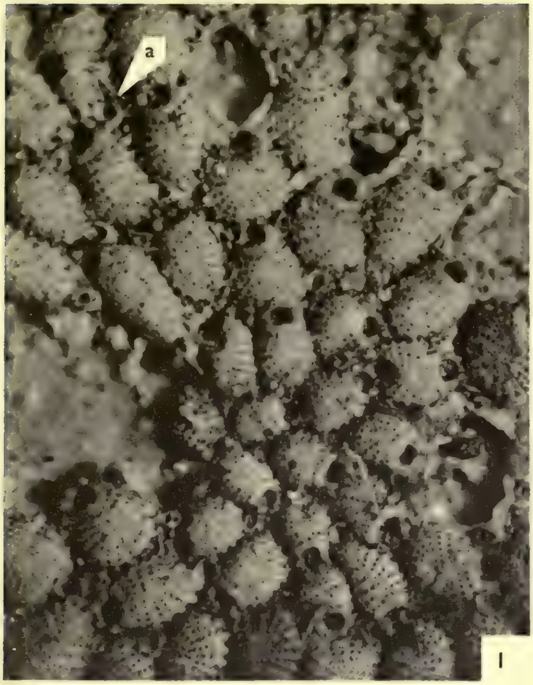
Fig. 2. Ancestrula (*A*), young and adult zooecia with paired, distally pointed and directed avicularia. ×20. D.8003.

Castanopora jurassica (Gregory)

Fig. 3. Very worn specimen. Adult zooecia with large, oval, interzooecial avicularia (*a*). ×20. D.3313.

Fig. 4. Adult zooecia. Holotype of *Rhiniopora scabra* Lang. ×20. D.14207.

Fig. 5. Worn and damaged zoarial fragment partly embedded in matrix, but with one complete frontal shield, on what is probably a young zooecium, and large, oval, sporadic, interzooecial avicularia (*a*). Holotype of *Castanopora jurassica* (Gregory). ×20. D.180.



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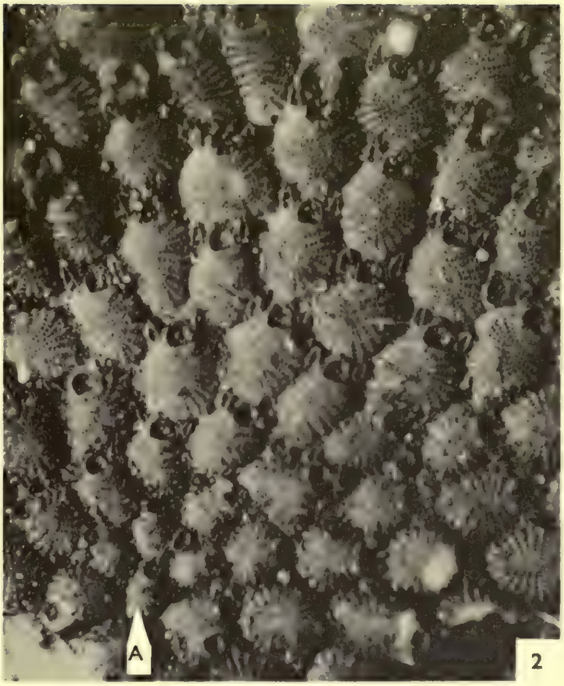

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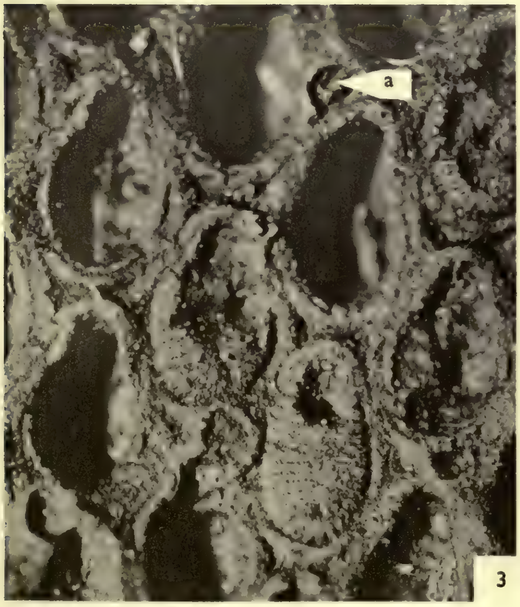

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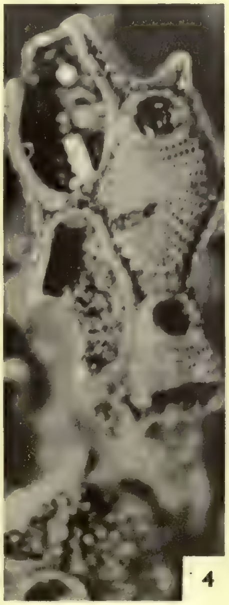

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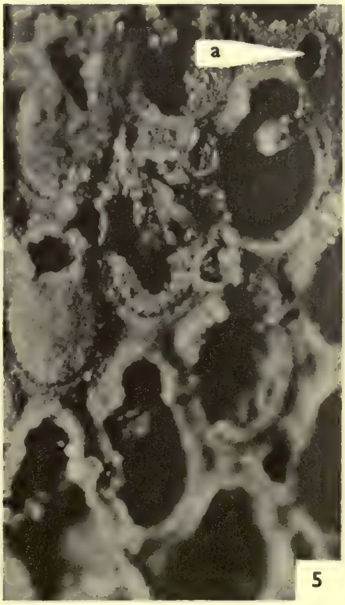

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CASTANOPORA

PLATE 18

Castanopora glandulosa Lang

FIG. 1. Adult zooecia with paired avicularia (*a*). Holotype. ×20. D.15009.

Castanopora magnifica (d'Orbigny)

FIG. 2. Adult zooecia with interzooecial avicularia. ×20. N.C.M.76.937 (26/1).

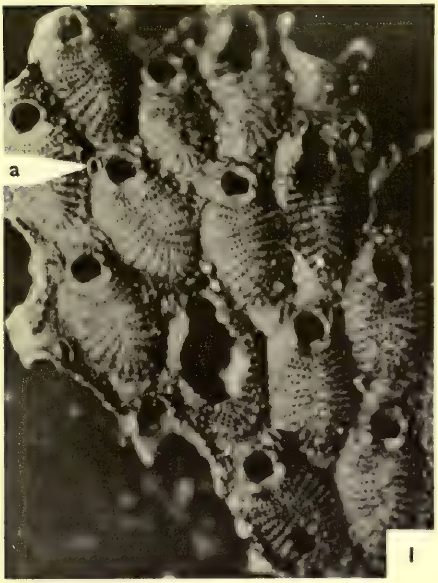
FIG. 3. Adult zooecia with prominently thickened apertural bars. ×20. N.C.M.76.937 (27/4).

FIG. 4. Large, well-preserved adult zooecia. ×20. D.40673.

FIG. 5. Large zooecia, one with broken ovicell (*o*). ×20. S.M., B.36266. Figured Brydone (1913, pl. 14, fig. 8) as *Cribrilina cacus* and assigned to *Rhiniopora* by Lang (1922 : 193).

FIG. 6. Adult zooecia with interzooecial avicularia. Holotype of *Rhiniopora aspera* Lang. ×20. D.15620.

FIG. 7. Adult zooecia. ×20. D.14176. Labelled by Lang "*Rhiniopora asperula* (Marsson)".



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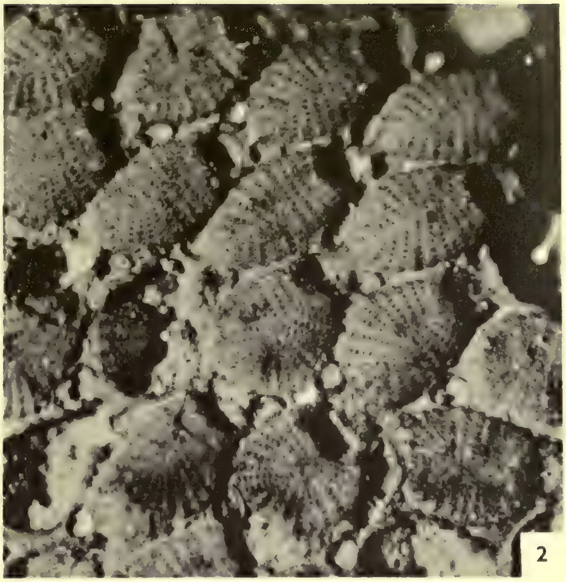

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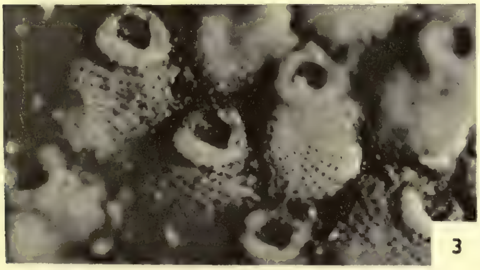

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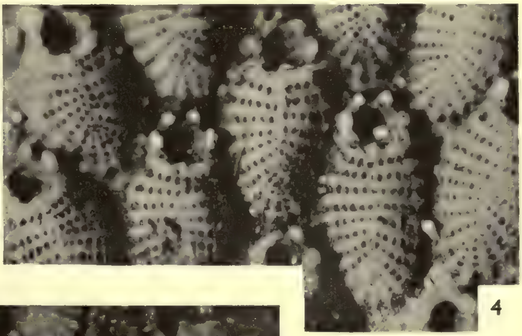

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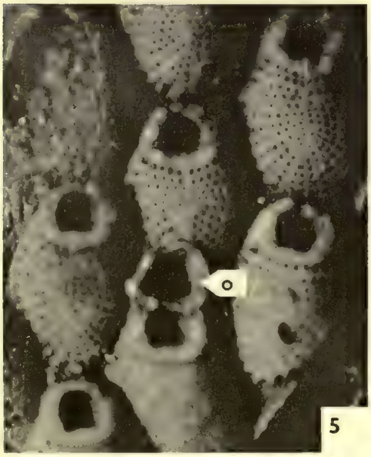

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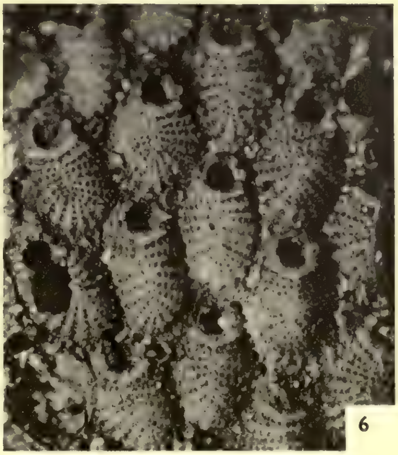

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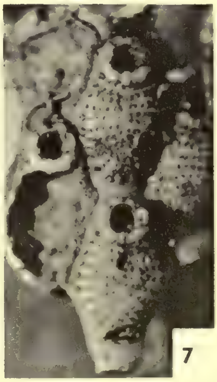

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CASTANOPORA

PLATE 19

Castanopora magnifica (d'Orbigny)

FIG. 1. Well-preserved, large, adult zooecia, several totally regenerated (*R*) after damage to frontal shield. ×20. S.M., B.36264. Figured Brydone (1913, pl. 14, fig. 6) as *Cribrilina cacus* and tentatively assigned to *Rhiniopora aspera* by Lang (1922 : 188).

FIG. 2. Adult zooecia with oval, interzooecial avicularia. ×20. N.C.M.76.937 (27/1).

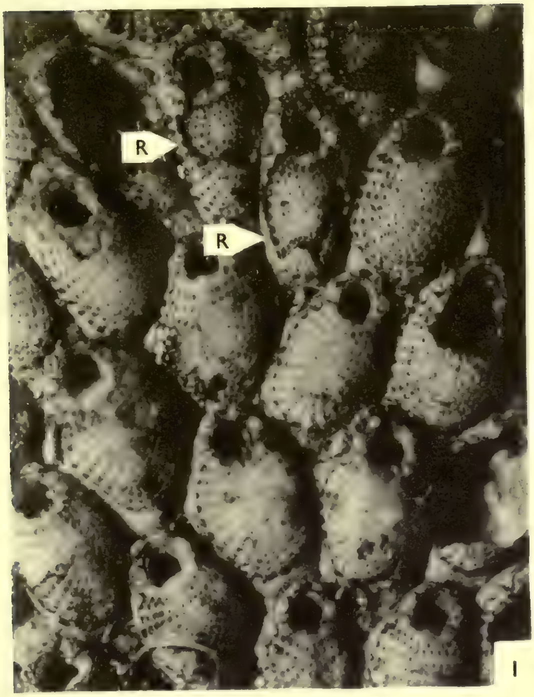
FIG. 4. Large, well-preserved, adult zooecia with four or five oral spine-bases. ×20. S.M., B.36265. Figured Brydone (1913, pl. 14, fig. 7) as *Cribrilina cacus* and chosen by Lang (1922 : 193) as lectotype of *Rhiniopora cacus* (Brydone).

FIG. 5. Adult zooecia. Holotype of *Rhiniopora horrida* Lang. ×20. D.14171.

FIG. 6. Adult zooecia with long, oval avicularium (*a*). ×20. N.C.M.76.937 (27/1).

Castanopora aviculosa Lang

FIG. 3. Adult zooecia with marked proximal-lateral constrictions in the orifices and frequent, variously directed, pointed avicularia. Copy of a photograph in the British Museum (Natural History) of a specimen in the F. Canu Collection, Paris.



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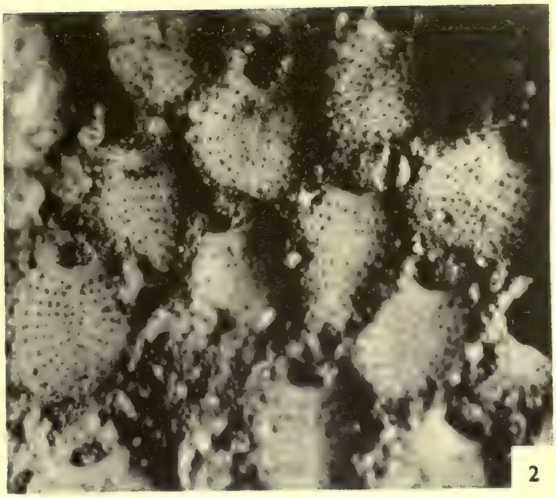

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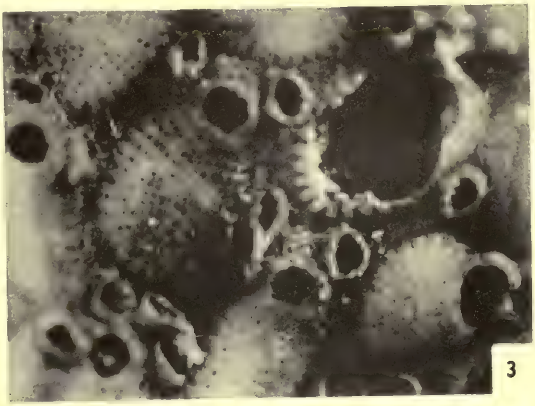

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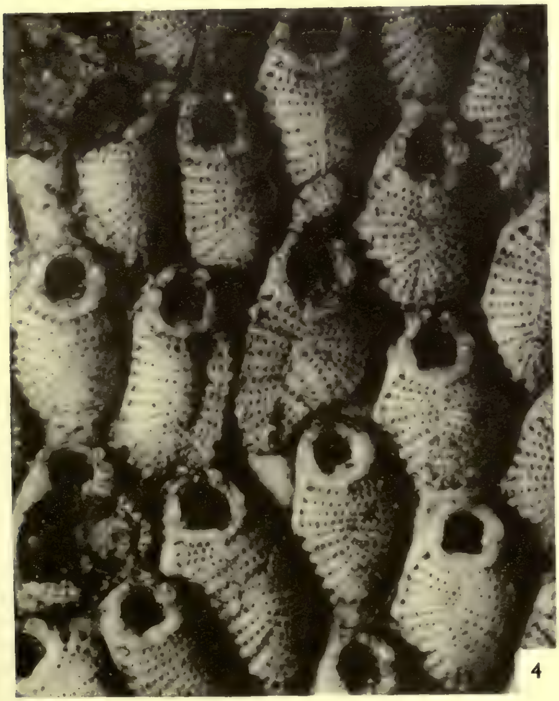

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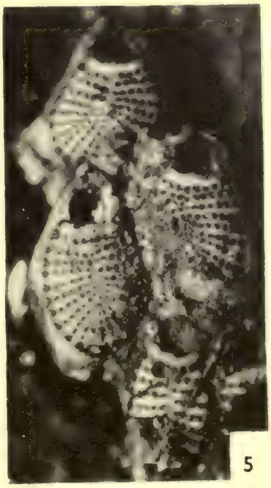

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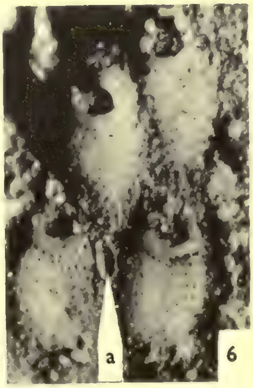

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CASTANOPORA

PLATE 20

Castanopora magnifica (d'Orbigny)

FIG. 1. Large adult zooecia, with large, oval, interzooecial avicularia. Copy of part of a photograph by P. Mémin (Serv. Photo. Géol. E.N.S.) of d'Orbigny Collection No. 7992, Paris. Holotype (?). ×25.

Ubaghsia ranunculus (Lang)

FIG. 2. Adult zooecia, one with unbroken proximal oral shield (*pos*). Holotype. ×20. D.23388.

Ubaghsia aurita (Lang)

FIG. 3. Group of adult zooecia. Copy of a photograph in the British Museum (Natural History) of the holotype in the F. Canu Collection, Paris.

Ubaghsia gasteri sp. nov.

FIG. 4. Adult zooecia. Paratype. ×20. D.40548.

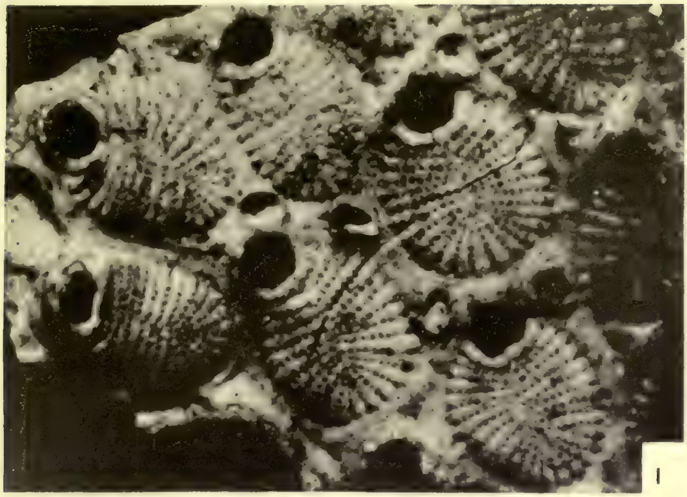
FIG. 7. Adult zooecia, with large, paired lateral oral avicularia (*a*), forming part of the proximal oral shield, and occasional small, round, sporadic avicularia (*b*). Holotype. ×20. D.40546.

Ubaghsia crassa (Lang)

FIG. 5. Group of adult zooecia. ×20. N.C.M.76.937 (30).

Ubaghsia coaxans (Lang)

FIG. 6. Two adult zooecia with broken and worn proximal oral shields. Holotype. ×20. D.14209.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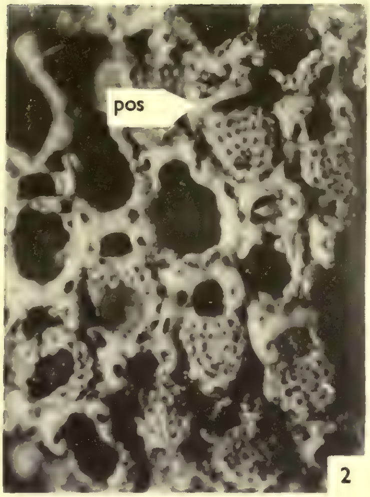

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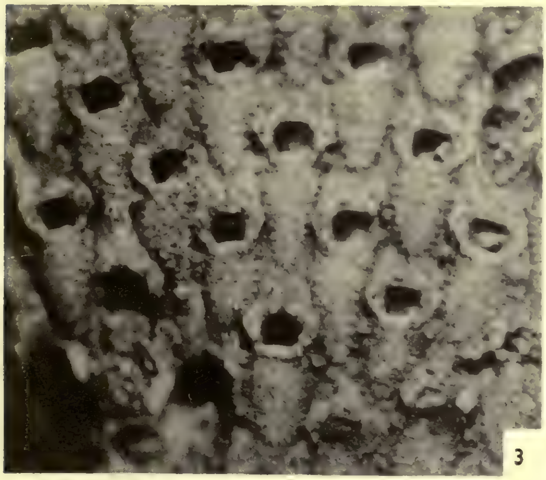
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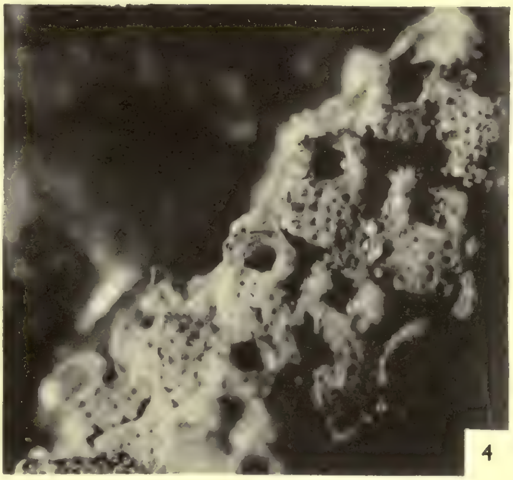
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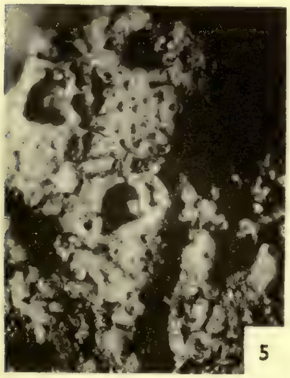
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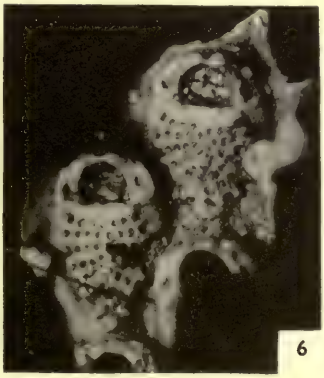
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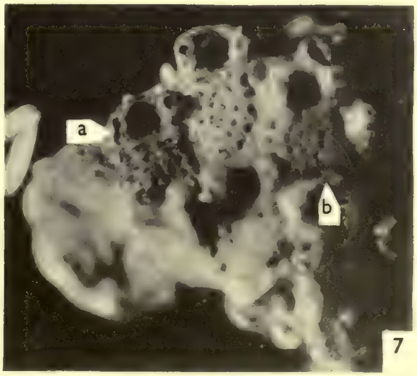

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CASTANOPORA, UBAGHSIA

PLATE 21

Ubaghsia reticulata (Ubaghs)

FIG. 1. The frontal shields of the adult zooecia are in focus, a fragment of tertiary front wall (*W*) is blurred. ×20. D.1391. Labelled by Lang " *Batrachopora ornata* (Goldfuss) ".

FIG. 2. The fragment of tertiary front wall (*W*) is shown in focus above the zooecia. ×20. D.1391.

FIG. 3. Adult zooecia ; the orifices are almost as large as the frontal shields. Holotype of *Batrachopora hyla* Lang. ×20. D.11852.

Ubaghsia langi sp. nov.

FIG. 4. Ancestrular area. Holotype. ×20. N.C.M.247.956 (4/1).

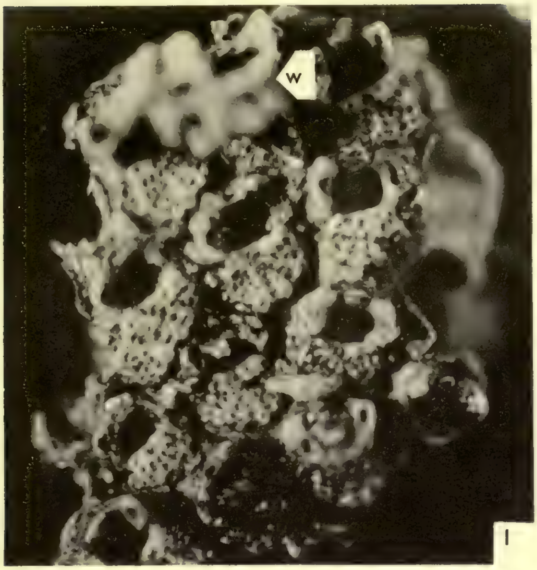
FIG. 5. Group of adult zooecia. Holotype. ×20. N.C.M.247.956 (4/1).

Ubaghsia coaxans (Lang)

FIG. 6. Three damaged, worn adult zooecia. Paratype. ×20. D.15041.

Ubaghsia crassa (Lang)

FIG. 7. Worn, adult zooecium. Holotype. ×20. D.16674.



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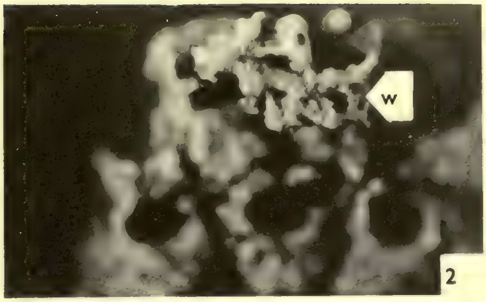

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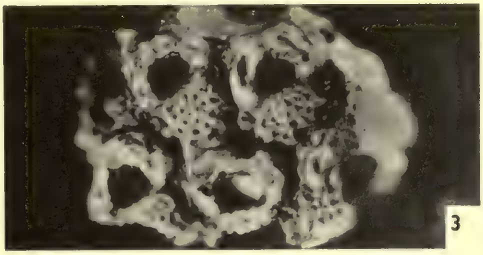

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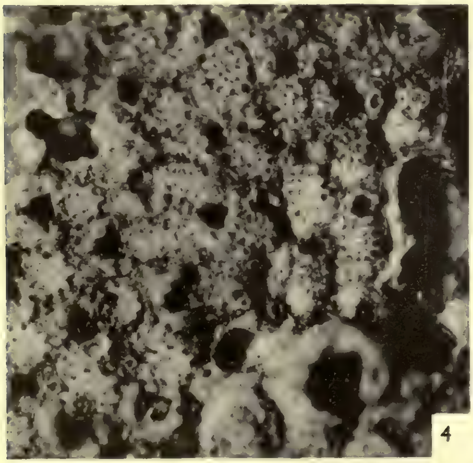

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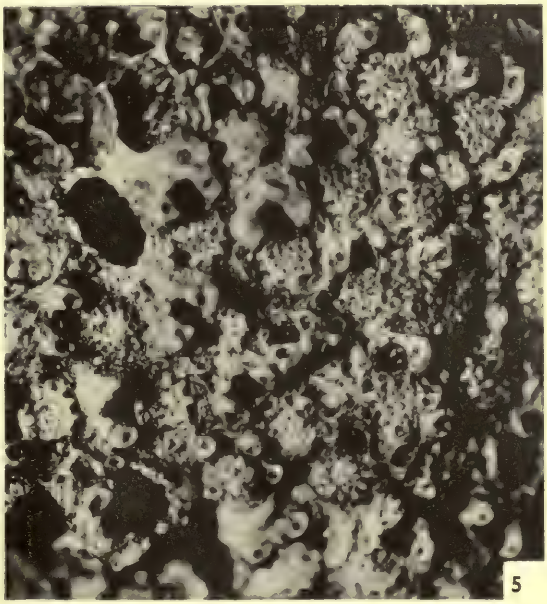

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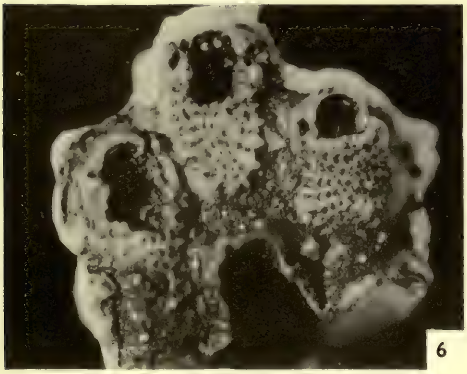

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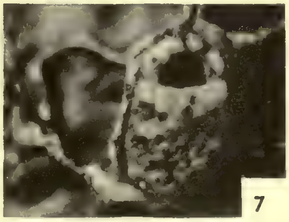

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UBAGHSIA

PLATE 22

Ubaghsia ocellata (Jullien)

FIG. 1. Adult part of zoarium showing bifurcated distal oral spines and, in the lower part of the figure, the complete tertiary front wall. Copy of part of figure by Jullien (1886, pl. 19, fig. 1).

FIG. 2. Vertical section through the unilaminar zoarium. Copy of figure by Jullien (1886, pl. 19, fig. 3).

Ubaghsia meudonensis (Jullien)

FIG. 3. Adult part of zoarium lacking tertiary front wall. Copy of part of figure by Jullien (1886, pl. 17, fig. 1).

FIG. 4. Three adult zooecia lacking tertiary front walls, showing an interzooecial avicularium between the two zooecia at the top. Copy of part of figure by Jullien (1886, pl. 17, fig. 4).

Ubaghsia demorgani (Jullien)

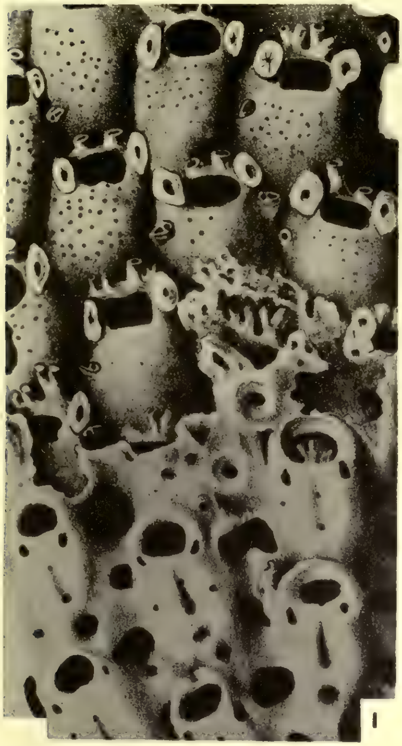
FIG. 5. Part of adult zoarium with complete tertiary front wall. Copy of part of figure by Jullien (1886, pl. 19, fig. 4).

FIG. 6. Part of adult zoarium with tertiary front wall largely removed. Copy of part of figure by Jullien (1886, pl. 19, fig. 5).

Ubaghsia reticulata (Ubaghs)

FIG. 7. Part of adult zoarium lacking a tertiary front wall in lower part of the figure. Copy of part of figure by Jullien (1886, pl. 18, fig. 4).

FIG. 8. Worn, adult zooecia with two interzooecial avicularia. Copy of part of figure by Jullien (1886, pl. 18, fig. 5).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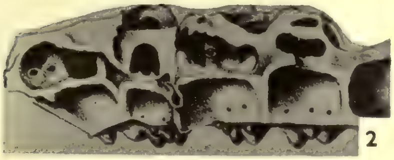
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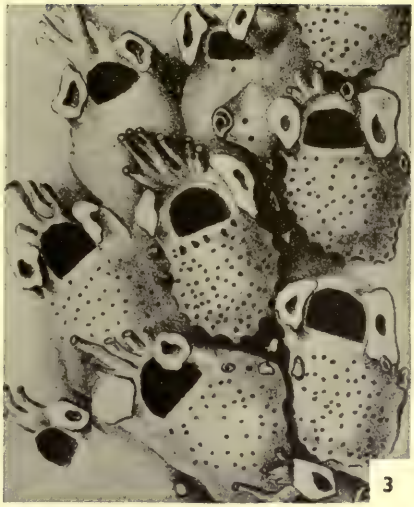
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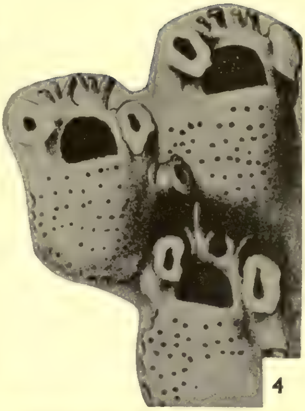
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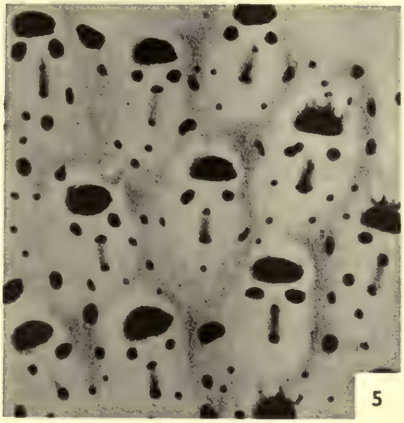
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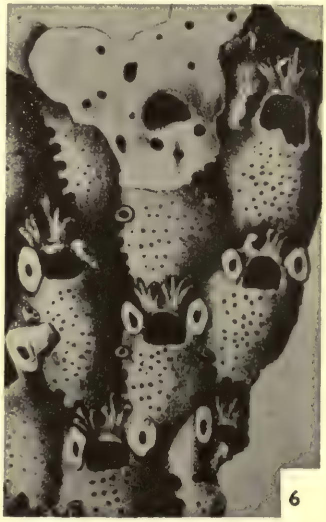
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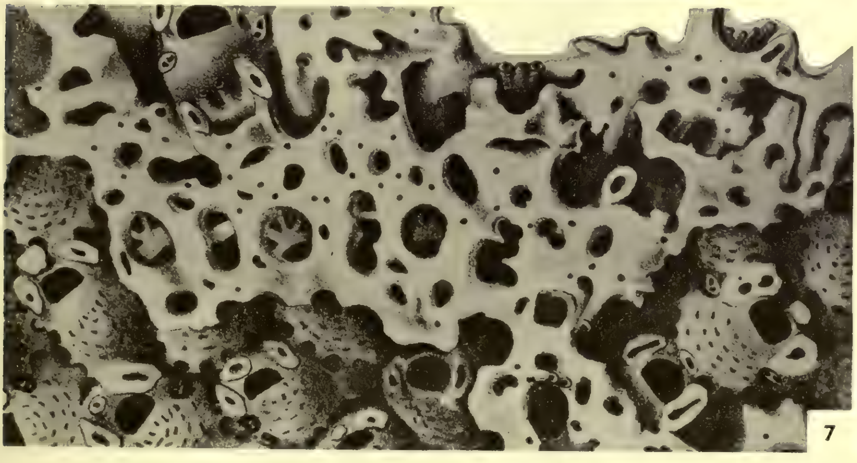
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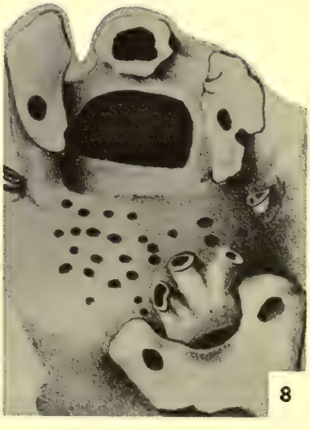
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UBAGHSIA

PLATE 23

Ubaghsia ornata (Goldfuss)

FIG. 1. Worn, adult zooecia with very large orifices. The zooecium (*Z*) on the left has only four costae. × 20. D.19357.

FIG. 2. Somewhat worn, adult zooecia with very large orifices and few costae. The zooecium (*Z*) has only three costae. × 20. D.8529.

FIG. 3. *Ubaghsia* ? *ornata* (Goldfuss). Worn adult zooecia. × 20. D.28526.

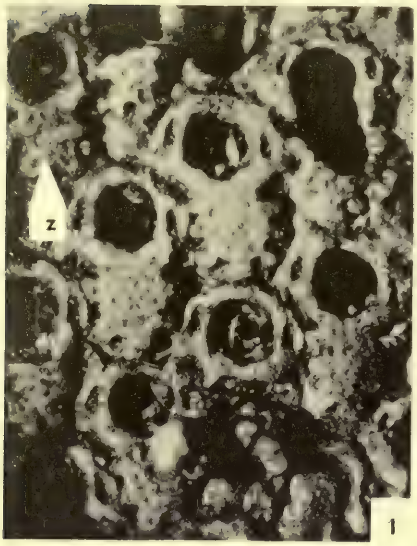
FIG. 4. Adult zooecia with orifices as large as the frontal shields, with paired, pointed, oral avicularia (*a*) and small rounded interzooecial avicularia (*b*). × 20. D.19356.

Andriopora major sp. nov.

FIG. 5. Caudate, adult zooecia. Holotype. × 20. D.39418.

Andriopora minor sp. nov.

FIG. 6. Adult zooecia, some ovicelled (*o*). Holotype. × 40. D.39417.



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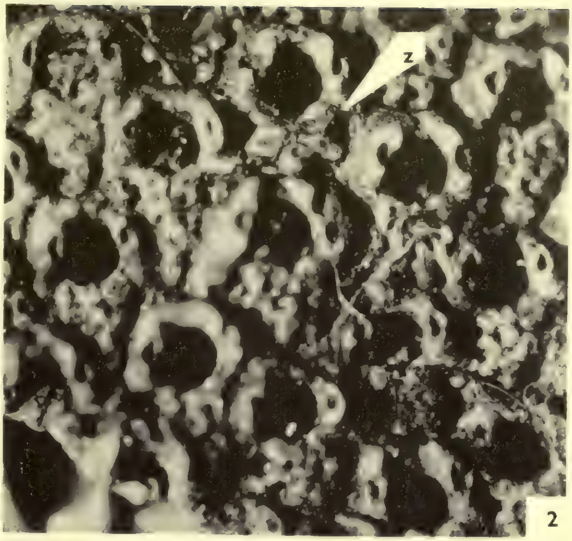

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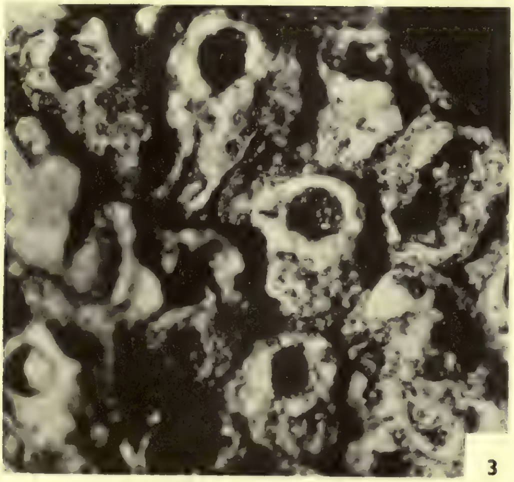

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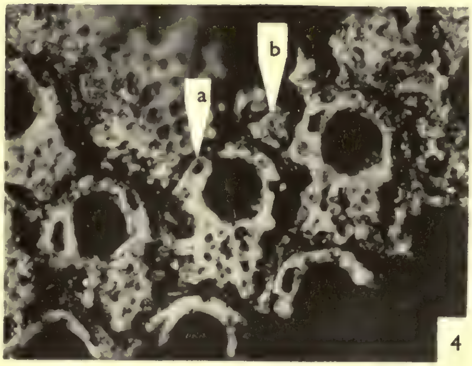

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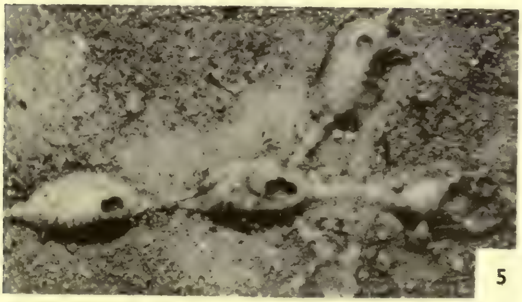

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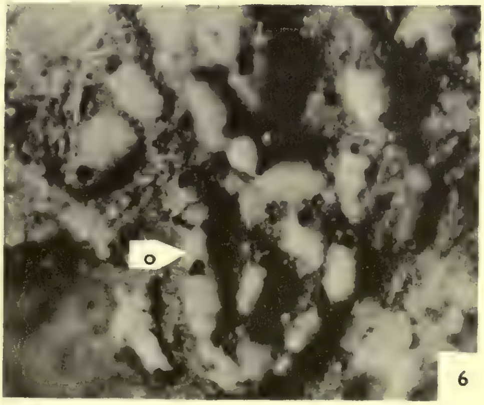

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UBAGHSIA, ANDRIOPORA

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12 JUN 1962
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ON *PTERUCHUS*, A MICROSPOROPHYLL OF THE CORYSTOSPERMACEAE

12 JUN 62

J. A. TOWNROW

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 6 No. 2
LONDON: 1962

ON *PTERUCHUS* A MICROSPOROPHYLL OF THE CORYSTOSPERMACEAE

BY

JOHN A. TOWNROW

(University of Tasmania)

12 JUN

Pp. 287–320 ; *Pls.* 24–26 ; 11 *Text-figures*

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ON *PTERUCHUS* A MICROSPOROPHYLL OF THE CORYSTOSPERMACEAE

By J. A. TOWNROW

SYNOPSIS

Three species of *Pteruchus* are redescribed, *P. africanus* Thomas, the type species, *P. dubius* Thomas and *P. simmondsi* (Shirley) Thomas. The material comes from Burnera Waterfall, Upper Umkomaas, Natal, and is of Molteno (Middle Triassic) age. A number of species are merged with *P. africanus*. The specimen originally named *Pteruchus edwardsi* Thomas is transferred to *Stachyopitys*. The ascription of *Pteruchus* to the *Dicroidium–Xylopteris* group of leaves, and the morphology of *Pteruchus*, are discussed. *Pteruchus* is compared with a number of other pollen organs, but is distinct from all.

INTRODUCTION

Pteruchus was first described as a separate genus by Dr. H. Hamshaw Thomas (1933). He believed it to be the pollen organ of the extremely abundant Triassic forking leaves here called the *Dicroidium-Xylopteris* group. This term is meant to include the ten or so leaf-species placed in *Dicroidium* (Jakob & Jakob, 1950; Townrow, 1957) and the three species of *Xylopteris* (Jones & Jersey, 1947 under the name *Stenopteris*, and also p. 308). New information is now brought forward which strongly supports some of Thomas' conclusions, particularly the ascription of *Pteruchus* to the *Dicroidium-Xylopteris* group; but is against some other of his views, e.g. the limits of the several species of *Pteruchus*. It enables one to take up a definite stand on some points, in particular, on the morphology of *Pteruchus* which Dr. Hamshaw Thomas was obliged to leave uncertain.

The material examined consists of Thomas' material, and further more abundant specimens from the same locality, that is, from the Burnera Waterfall, Upper Umkomaas, Natal. This locality falls within the Molteno, and is of Middle Triassic age (Townrow, 1957 : 30, 31).

All type and figured specimens of *Pteruchus* are in the British Museum (Natural History) and are referred to by their British Museum registration numbers.

Genus **PTERUCHUS** Thomas, 1933 : 232

EMENDED DIAGNOSIS. Microsporophyll borne singly, without subtending organ, on cutinized axis of about same size as rachis. Axis radially symmetrical, cuticle showing similar rectangular cells all over. Microsporophyll, unforked alternate pinnate. Rachis showing lateral wing, and occasional vegetative pinnules, cuticle dorsiventral. Pinnae expanding into rounded or elongate lobed sporangial heads Heads more or less dome-shaped, non-sporangial surface often rugose. Venation pinnate, shown on sporangial side of heads. This surface completely occupied by pollen sacs : non-sporangial surface covered with cuticle. Pollen sacs borne over central part of head, but absent over thin margins and lobes and over continuation of pinna on to head. Pollen sacs numerous, more or less cigar-shaped, 0·75 mm. to 2·5 mm. long and 0·75 mm. to 1·5 mm. wide, unilocular, dehiscing by longitudinal slit, wall at maturity consisting of epidermis only, composed of narrow longitudinally elongated uniform cells, sometimes with slightly sinuous outlines. Cuticles of all parts delicate, about 1 μ thick, showing faint to pronounced, normally slightly, sinuous cell outlines, and rarely papillae ; cells more or less in rows over rachis and pinnae, without apparent orientation over heads. Stomata few, about 5/mm.^{2} over heads, exposed or sunken, normally flanked by two lateral and two terminal subsidiary cells, encircling cells normally distinguishable. A few usually tricellular pointed hairs present. Pollen bisaccate, sacci slightly to distinctly offset distally, overlapping or not, on to proximal face of body of grain, longer than wide, as long as or slightly shorter than body, normally more or less parallel sided and ornamented with moderately distinct reticulum, meshes 2 μ to 3·5 μ wide, walls of mesh about 1 μ thick. Body of grain about 50% longer than wide, ends obtuse or bluntly pointed, rarely round, wall between body and sacci normally distinct, body minutely reticulate or almost smooth. Distinct sulcus present, flanked by strip of thicker cutin, about as long as body, not occupying whole space between sacci on distal surface.

Length : 50 μ (typical).
Total width : 80 μ (typical).
Ratios (means) : Length of body/width of body, 1·27.
Width of whole grain/length of body, 1·54.
Length of body/width of saccus (to distal roots), 1·25.

TYPE SPECIES. *Pteruchus africanus* Thomas.

DESCRIPTION. There are two difficulties presented by the Waterfall material. The first is that the specimens split through the fossil, leaving about equal quantities of plant material on both part and counterpart, which are thus mirror-images. This is an important point for it means that the part and counterpart as they stand cannot be superimposed directly, but to see one surface of the organ the part and a *transfer* of the counterpart must be superimposed (Text-fig. 2A, B). The second is that when macerated, the material, especially if of thick substance, breaks up into small fragments only a millimetre or so square. This is probably because the cuticle is too delicate to hold the coaly substance together when it swells in acid. Hence cuticle data have to be put together from very small pieces, and few stomata, for example, are seen on any one specimen.

The sporophylls are unforked and pinnate, the pinnae being offset towards the upper (adaxial) surface of the rachis (Pl. 24, fig. 4 ; Text-figs. 2D, 4H). In the small *P. simmondsi*, and the smaller specimens of *P. africanus* this is not obvious, although it can be deduced from the course of the cellular striae of the pinnae, which are interrupted by the lower surface of the rachis, but viewed from the upper surface, continue on to the rachis (Text-figs. 2D, 4H). This feature, together with the pinnate habit, and the lateral wing on the rachis, imparts bilateral symmetry to the organ.

Two specimens of *P. africanus* were still attached to short lengths of axis (Pl. 25, (fig. 2 ; Text-fig. 1B) : one specimen of *P. dubius* is probably similar (Pl. 24, fig. 6)

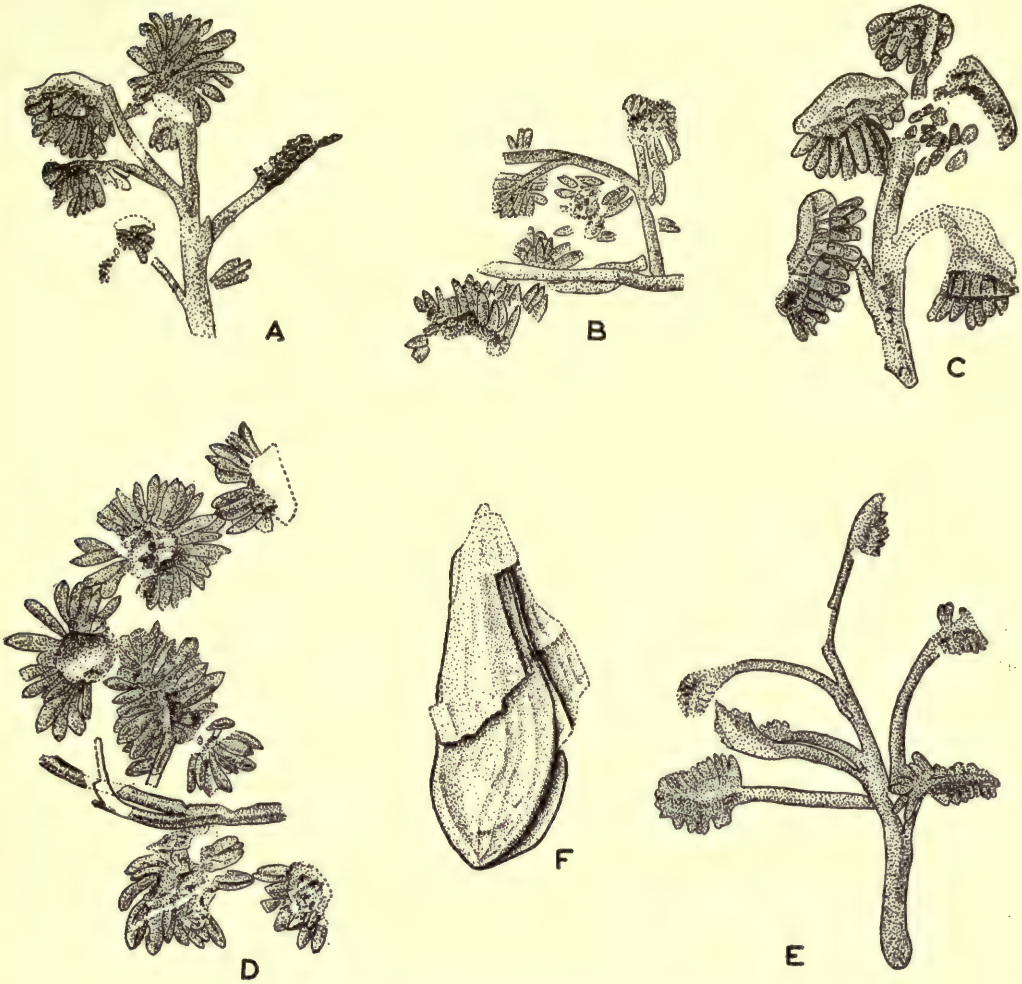

FIG. 1. *Pteruchus africanus, P. dubius*

A–D, *P. africanus.* A, sporophyll with some heads pointing towards the base of the organ, showing rugose non-sporangial surface of heads, a divided pinna, and, in heads with pollen sacs pointing downwards, undisturbed cell rows on the pinnae. V.42684. ×2·5. B, two sporophylls, one attached to a piece of the axis (running horizontally) and one detached. V.42688. ×2·5. C, sporophyll (*P. peltatus*) showing marginal attachment of pinna in uppermost and lowest right-hand heads. V.23386. ×2·5. D, sporophyll attached to a length of axis (running horizontally). V.42685. ×2·5.

E, *P. dubius.* Small complete sporophyll showing unforked habit and some divided pinnae. V.42686. ×5.

F, *P. africanus.* A pollen sac compressed laterally, showing dehiscence slit. The specimen is partly overlain by another pollen sac. ×25.

while one specimen of *P. simmondsi* had bits of cutinized plant matter, possibly of, the axis, sticking to the base of the rachis. The two specimens of *P. africanus*, and probably the specimen of *P. dubius* also, are attached singly, not in a cone or " flower ", and either at right angles to the axis, or else curving away from it at a wide angle. Other specimens of all three species showing the sporophyll base often (8 out of 11) show a curvature, suggesting that the sporophyll normally came to lie at a wide angle to the axis.

None of the attached specimens shows any subtending organ on the axis, nor any sign of one such as a scar.

The central part of the axis is raised but the organ does not show strong relief. It does not show a wing (Pl. 25, fig. 2). The cuticle is extremely thin, but shows somewhat obscure outlines of rectangular cells all over, and again, no sign of a wing (cf. p. 313). It was therefore radially symmetrical (at least externally). The fact that the organ is cutinized and of low relief suggests that it had not undergone much secondary thickening, and, a connected point, that lignified tissue was not massive.

The rachis cuticle is different. It is dorsiventral, showing on the lower surface more or less uniform elongated cells and very few or even no stomata. Similar elongated cells, devoid of stomata, are present over the wing on both surfaces. On the upper surface there is an ill-defined stomatal band, in which the cells are more nearly square, and the stomata are set obliquely, or even at right angles to the rachis long axis (Text-figs. 9B–D, 10B, C). This dorsiventrality is more marked in the larger specimens, though discernible in all.

In all the species the rachis may be raised in irregular lumps, especially in the larger specimens (Pl. 24, figs. 4, 6 ; Text-figs. 1C, 4H). The lumps leave no trace on the cuticle, and after treatment with acid, stand out as areas of darker matter. They must be wholly internal and are possibly nests of thickened cells.

The pollen sacs almost certainly pointed towards the base of the organ. In some specimens they are so preserved (Pl. 24, fig. 3 ; Text-fig. 1A, C), and here the cell rows on the pinnae are not twisted. But in the more numerous specimens in which the heads are rotated in various ways the cell rows are twisted (Text-figs. 2D, 4H).

Vegetative pinnules are rare, they occur in only six of the fifty-one specimens available (*P. africanus* (4), *P. simmondsi* (1), *P. dubius* (1)) and, with two exceptions (V.23360, V.42683) these specimens showed only a single pinnule each. One pinnule of *P. dubius* (V.42683) is set just above the point at which the first pinna (divided in this specimen) arises (Text-fig. 4C). The others lie at varying levels between the sporophyll base and the first pinna. None subtend anything (Pl. 26, fig. 6 ; Pl. 25, fig. 1 ; Thomas, 1933, text-fig. 40). In one specimen of *P. africanus* (V.23360), there are two pinnules near the sporophyll base, lying one about 1 mm. above the other (Text-fig. 3B). I cannot find the two minute pinnules figured by Thomas (1933, text-fig. 36) in the specimen called *P. papillatus*, while in the specimen he states showed a basal pair (p. 236) only one is now seen, and there is no clear impression of a second (Pl. 26, fig. 6).

The sporangial heads show the same basic plan, though they differ in proportions and detail (pp. 298, 300, 303). They are attached marginally, though, rather as in a pelargonium leaf, the attachment is mainly on the under (sporangial) side, and may

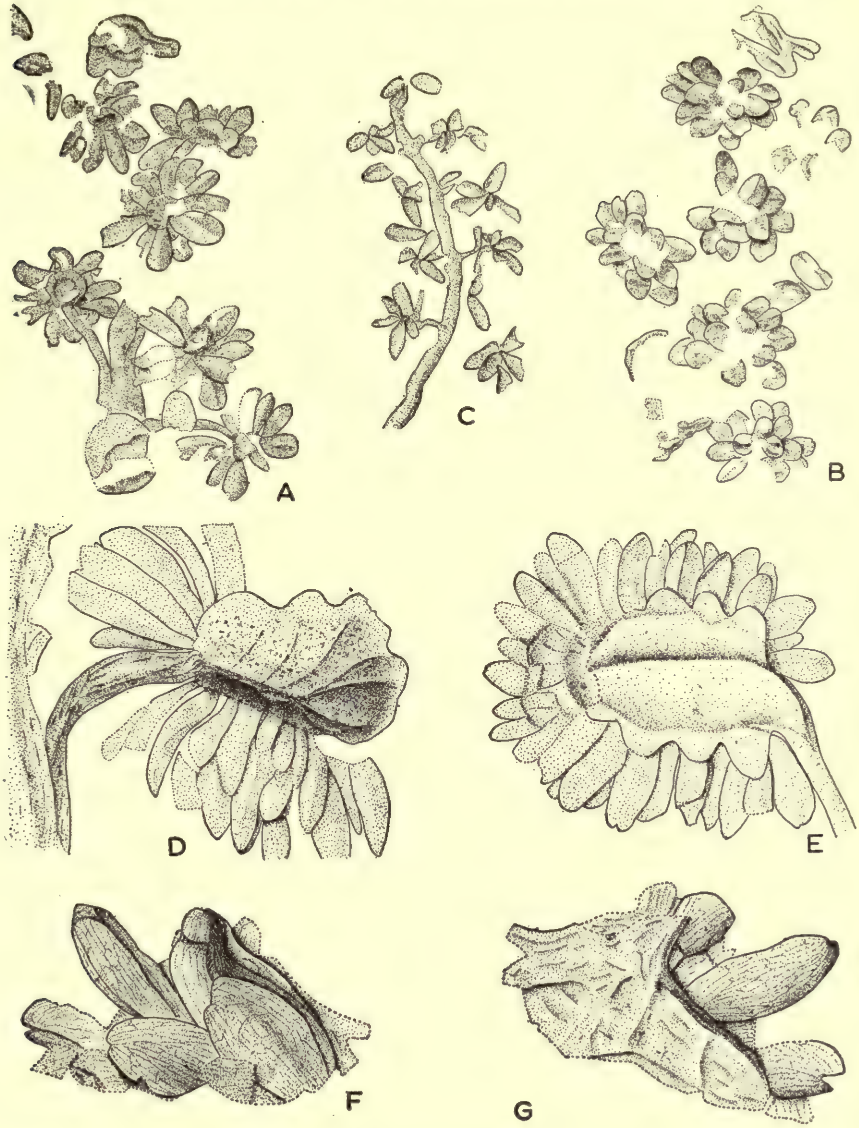

FIG. 2. *Pteruchus simmondsi*, *P. africanus*

A–C, *P. simmondsi*. A, B, part and transfer of the counterpart of a sporophyll showing swollen base (probably with fragments of axis attached) and, at top, a head compressed laterally, showing smooth non-sporangial surface. V.42687. ×3·75. C, small sporophyll showing branching and with (almost certainly) only some of the pollen sacs originally present. V.42691. ×3·75.

D–G, *P. africanus*. D, sporangial head showing sporangial surface almost free of pollen sacs, vascular ridges with rows of elongated cells along their crests, area of pollen sac attachment and twisted cell rows on pinna, interpreted as a consequence of rotation of head into the bedding plane. Specimen seen from under (adaxial) surface. Note pinna interrupted by edge or rachis. V.42682. ×7. E, sporangial head, seen from non-sporangial surface, showing marginal attachment of pinna and marginal lobes. Surface of head nearly smooth. V.23384. ×7. F, G, same fragment, seen from sporangial (F) and non-sporangial (G) sides, showing form of pollen sacs, cell rows on them and their dehiscence slits. ×3·5.

be overlapped by the marginal lobes (Pl. 25, fig. 3 ; Pl. 26, fig. 12 ; Text-figs. 2D, 4A, G). Thomas suggested (1933 : 238) that the specimen named *P. peltatus* (V.23386) was peltate. This I believe to have been an error. The specimen is refigured in Text-fig. 1C ; two heads show their marginal attachment, and a transfer shows another was the same ; the others do not show their attachment at all.

Pteruchus seems to have been shed as a complete organ, without disarticulating, shedding its pollen sacs, or even all its pollen. There are thus few heads showing their sporangial surface unobscured by pollen sacs. There are eight sporangial heads preserved in this way in *P. africanus*, some incomplete. The sporangial surface is raised in ridges, one ridge more or less opposite each marginal lobe, which coalesce near the point of attachment (Pl. 26, figs. 9, 10 ; Text-figs. 2D, 3C). In two heads, lines of elongated cells were plain, running along the top of these ridges (Text-figs. 2D, 3C) which therefore almost certainly mark the course of the veins. The veins are pinnate, based upon a first division of the main vein near its base into three nearly equal parts, fanning out from the point of attachment (Pl. 26, fig. 10). Over most of the heads, the surface is rough, sometimes raised in little rings about 1 mm. in diameter, but usually showing no distinct pattern. It seems likely that these rings and the rough area in general, mark the insertion of the pollen sacs. It is not clear whether the pollen sacs had any definite arrangement. Usually none is apparent, but in one place (Pl. 26, fig. 9) the rings seem to run in rows parallel with a vein. I can find no evidence that the pollen sacs were borne in groups. Over most of the lobes, around the margins, in areas extending as embayments between the vascular ridges and over the " midrib ", i.e. the continuation of the pinna on to the head, the surface is smooth and presumably devoid of pollen sacs (Pl. 26, fig. 10 ; Text-figs. 2D, 3C). Except for a rim, the sporangial surface is uncutinized (Pl. 26, fig. 7) while the number of pollen sacs and the very close-set arrangement of the little rings (where visible) indicate that the pollen sacs were closely packed together, so that there was no epidermal tissue between them.

In the other species the evidence is much less clear. One head of *P. simmondsi* is largely free of pollen sacs, and shows ridges with elongated cells over them, probably set in a pinnate pattern, as in *P. africanus* (Text-fig. 4H), and other heads show that the main vein at least was free of pollen sacs (Pl. 26, fig. 12). I have not seen any heads of *P. dubius* with their sporangial surface unobscured, but several heads show that the main vein at least was free of pollen sacs, as were the marginal lobes (Pl. 25, fig. 3).

Although the evidence is not complete, it is most likely that the heads in all three species were constructed on the same pinnate plan, as indicated by the veins. This is an important point, for it means that the heads were also bilaterally symmetrical and dorsiventral. The heads can thus be described as showing elongated sori over the veins, which become concrescent where the veins join up. I do not know why elongated cells along the vascular ridges are shown in two heads, but not in others. Perhaps the veins became displaced during fossilization.

The non-sporangial surface of the heads is strongly wrinkled in *P. africanus*, slightly so in *P. dubius* and hardly at all in *P. simmondsi*. I believe that some of this wrinkling existed in life (pp. 298, 303), some, however, is almost certainly caused by the compression of a thick organ. This wrinkling is apt to obscure the cell outlines of the cuticle of the head, especially over the centre of the head, the lobes and margins being, even in *P. africanus*, scarcely wrinkled at all (Pl. 26, fig. 7). As far as can be made out, both cells and stomata lack any preferred orientation, a useful point distinguishing marginal lobe from pollen sac (p. 303 and Text-fig. 10A; Thomas, 1933, text-fig. 48).

The pollen sacs dehisced by a longitudinal slit often (but by no means always) directed towards the centre of the pollen sac group. It also often extends a little way on to the dorsal surface of the pollen sac, so that, in sacs seen dorsal surface uppermost (the majority) it may appear like an apical nick. This has been taken for a terminal pore (Thomas, 1933 : 234), but a transfer reveals its nature, which is confirmed from the cuticle, and also shows a slit down one face (Text-fig. 2F, G). Seen as transparencies, e.g. in transfer, the pollen sac wall is composed of one layer of cells, corresponding to those seen on the cuticle from the pollen sac, and therefore epidermal (Pl. 26, fig. 11; Text-fig. 6D). The periclinal walls as seen in transfer are about 15 times as thick as the cell outlines seen on the cuticle. They may have been thickened. The cells are uniform over the whole pollen sac, except, possibly, next to the dehiscence slit. Here they may be narrower than elsewhere (Text-fig. 6K). However, this appearance may be caused by folding, which is almost invariably seen at this point.

It has been suggested that the pollen sacs were bilocular (Thomas, 1933 : 235), but there is convincing evidence that this is not so. Sections of pollen sacs from each species show only one loculus (Pl. 26, fig. 5), while the wall shows no sign of any partition, unlike a dehisced Angiosperm anther in which the partition between thecea is often visible. I have macerated about 80 pollen sacs, and have never seen more than one pollen mass. On the other hand, it is rather easy to macerate parts of two closely adherent pollen sacs, in which case the appearance described by Thomas could very well arise.

The cuticle of the three species is most variable in every character. In each it varies in thickness from about 1·5 μ down to so thin as to be almost impossible to prepare, probably less than 0·5 μ. In addition the stomata, even on one specimen, vary in the extent to which they are sunken. In general the most exposed lie on the lower heads or rachis (Text-figs. 8A–K). These two facts strongly suggest that the sporophylls were rather long lived, certainly not ephemeral, and that they varied in response to factors other than genetical, just like leaves for example. This view, however, is contrary to that of Thomas (1933 : 202).

The cell outlines may be faint or plain to see, but in either case are usually decorated with small sinuosities, consisting of projections about 1 μ long from the actual outline (i.e. the part occupied in life by the middle lamella) on to the general cuticle surface. In a few specimens of *P. africanus* the cells also bear a papilla (Text-fig. 9D; Thomas, 1933, text-fig. 37). The stomata are based upon the same plan in all three species; that is to say the guard cell poles lie more or less on the general cuticle surface, though in *P. simmondsi* they are sometimes overlapped by the terminal subsidiary cells (Text-fig. 8A), while the aperture is more or less sunken in a depression. The walls of the depression are formed by the lateral subsidiary cells, which are normally two, but may be divided into three or four. Quite unspecialized encircling cells are usually discernible, but may be absent, especially over the rachis (Text-fig. 9C, D).

The hairs are rare in all three species, scarcely 12 occur in any one specimen but all species show them. On the cuticle the hair base appears as a thickened ring (Text-fig. 6G ; Thomas, 1933, text-fig. 35) the area enclosed by the ring is sometimes

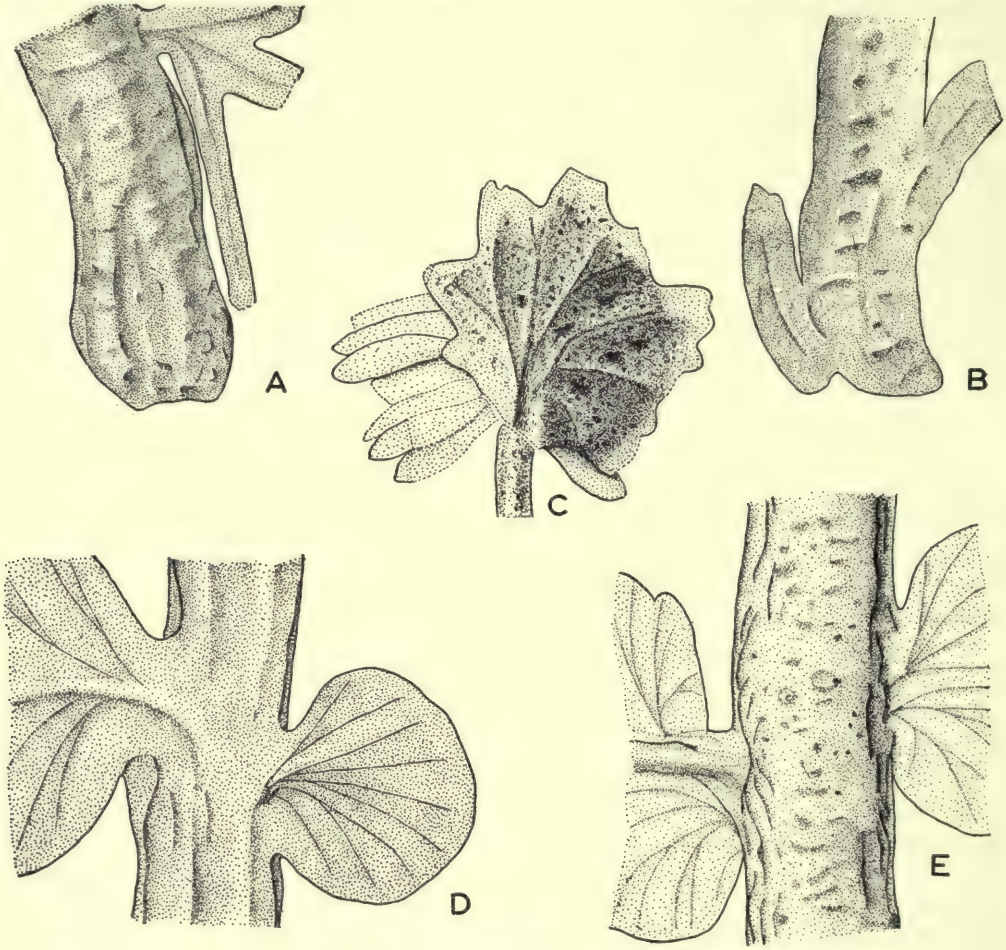

FIG. 3. *Xylopteris elongata*, *Pteruchus africanus*, *Dicroidium feistmanteli*

A, *X. elongata*. A leaf base showing large divided basal pinnule set a short way up from extreme tip of leaf (cf. Pl. 25 ; Text-fig. 5C). ×8.

B, C, *P. africanus*. B, sporophyll base (impression only) showing two alternate basal pinnules. V.23360. ×8. C, sporangial head, showing sporangial surface free of pollen sacs. It shows main vein, vascular ridges, area of pollen sac attachment, smooth margins and marginal lobes. V.42682. ×8.

D, E, *D. feistmanteli*. Equivalent portions of same leaf (E a transfer), drawn from upper (adaxial) (D) and lower (E) surfaces, showing that the pinnae are offset towards upper rachis surface, and venation. ×8.

thinly cutinized, sometimes open. On a transfer of the counterpart of a specimen, the hairs themselves may be found. Though often obscure they seem normally to be pointed, and to have three obliquely divided cells, as in Text-fig. 6J. I correlate the hairs with the hair bases on the cuticle, because, though rare, each can be found with regularity, and there is no other structure that I can find to which the hair bases might belong.

It proved difficult to obtain satisfactory pollen preparations of *Pteruchus*. Either the grains stuck together in a mass, obscuring the individuals, or else the pollen sacs were nearly empty, and some of the grains remaining were clearly strays. By breaking up the masses, and examining grains at their edges it was possible to obtain small samples (15 or 20 grains) from every specimen.

The grains are variable (see diagnosis and specific descriptions pp. 298, 300, 303, Pl. 26, figs. 1–4; Text-figs. 10D–G, 11). One of the most prominent features is the sulcus (here the term is confined to the presumed germination furrow lying between the distal roots of the sacci, and not occupying the whole distal surface of the body of the grain, see Erdtmann, 1947). In many grains the lips touch along their whole length, but in others, otherwise similar, the sulcus gapes open.

Pteruchus africanus Thomas

(Pl. 24, fig. 4, Pl. 25, figs. 1, 2, Pl. 26, figs. 2, 4–11; Text-figs. 1–3, 6–10)

1933 *Pteruchus africanus* Thomas, p. 235, pl. 24, figs. 71, 72, text-figs. 34, 35. Fig. of holotype pl. 24, fig. 71.
1933 *Pteruchus papillatus* Thomas, p. 237. pl. 24, fig. 77, text-figs. 36, 37. Pollen figd. pl. 24, fig. 77.
1933 *Pteruchus peltatus* Thomas, p. 238, text-figs. 38, 39.
1933 *Pteruchus hoegi* Thomas, p. 239, pl. 24 fig. 75, text-figs. 40, 41.
1933 *Pteruchus stormbergensis* Thomas, p. 241, text-fig. 43.
1933 *Pteruchus* sp. Type X, Thomas, p. 243, text-figs. 47, 48.

Specimens doubtfully identified.

1876 *Sphenolepis rhaetica* Geinitz, p. 12, pl. 2, figs. 23, 24.
1888 Male flower of *Baiera tenuifolia* Johnston, pl. 27, figs. 2D, E.
1890 *Trichopitys johnstoni* Feistmantel, p. 113, pl. 10, fig. 5. Johnston's specimen refigured.
1898 *Stachyopitys annularioides* Shirley, p. 13, pl. 18, fig. 1.
1917 *Stachyopitys annularioides* Shirley: Walkom, p. 13, pl. 4, fig. 6.
1925 Male flower of *Baiera tenuifolia* Johnston: Walkom, p. 85, text-figs. 15, 16. Johnston's Tasmanian material refigured.
1933 *Pteruchus annularioides* (Shirley) Thomas, p. 233. New name only.
1933 *Pteruchus minor* Thomas, p. 242, text-fig. 46. Small specimen regarded as indeterminable.
1933 *Pteruchus* sp. Type Y, Thomas, p. 243. No figure.
1947 *Pteruchus annularioides* (Shirley) Jones & Jersey, p. 55, text-fig. 38.
1947 *Pteruchus* sp. Jones & Jersey, p. 56. No figures.

Specimen regarded as distinct:

1947 *Pteruchus* cf. *africanus* Thomas: Jones & Jersey, p. 55, text-fig. 51.

HOLOTYPE. Brit. Mus. (N.H.) No. V.23384.

MATERIAL. H. Hamshaw Thomas Colln., Brit. Mus. (N.H) Nos. V.23360, V.23384–88, V.23390–94. J. A. Townrow Colln., Nos. V.42682, V.42684–85, V.42688–90, V.42797.

EMENDED DIAGNOSIS. Microsporophyll about 2 cm. long, rachis about 1·5 mm. wide at base. About eight (6–9) long, normally unbranched pinnae present. Heads round to about four times as long as wide, width about 5 mm.; non-sporangial surface strongly rugose, about 10 lobes per head, lobes small in proportion to size of head. Pollen sacs more than 30 per head, about 2·5 mm. long and 1·5 mm. wide. Cell outlines faint, 1 μ wide or less, sinuosities small, sometimes absent, about 1 μ long, usually obtuse, not pointed. Stomata somewhat sunken, poles exposed, pit not overlapped by cutin flanges. Pollen with sacci scarcely extending on to proximal surface of grain, usually shorter than body of grain, often slightly inflated. Body of grain sometimes bluntly pointed, reticulum on sacci normally conspicuous, meshes about 3 μ in diameter, walls about 1 μ thick; ornamentation on body faint or absent. Dimensions in μ (standard deviations bracketed): Length of body 46·25 (6·45); width of body 32·2 (7·45); length of sacci 35·2 (12·6); width of sacci 36·2 (9·2); height of grain 20 (2·8); total width of grain 63 (6·3).

DESCRIPTION AND REMARKS. The pinnae are almost always unforked, but in two specimens (V.42684, V.42707, Text-fig. 1A) certain pinnae branch on leaving the rachis. When compressed laterally (Text-fig. 1A) the heads appear dome-shaped and the non-sporangial surface is raised in irregular lumps. Probably, therefore, the wrinkling of the cuticle of the heads is not all connected with the compression of a thick organ, but is partly original. The pollen sacs, while varying consideraly in size and form, are normally not much inflated (Pl. 24, fig. 4; Text-fig. 2F, G).

Cell outlines are sometimes so faint that they are scarcely visible and, about one-third of the preparations lack them altogether. When present the sinuousities are small (1 μ or less) and grade gradually into the residue of the cuticle so that it is difficult to decide exactly where they end. (Text-fig. 7A). Text-fig. 8B, C show two stomata from the same specimen. One, Text-fig. 7B, comes from an upper head, the other, Text-fig. 8C from a lower head. Each is typical of the degree of sinking seen on upper and lower heads respectively. Stomata from a lower head, but sunken like Text-fig. 8B, or stomata from an upper head but nearly exposed like Text-fig. 8C number less than 1 in 6. Almost exposed stomata (Text-fig. 10) number about 1 in 5 on the marginal lobes of some lower heads.

In most pollen grains the insertion of the sacci is similar to that shown in Pl. 26, fig. 2, they do not extend on to the proximal surface of the body of the grain, but this character is a variable one, and some grains show overlap on to the proximal surface (Text-fig. 10F). As seen in tangential longitudinal view, the body of the grain is usually about as broad as high (Pl. 26, fig. 2; Text-fig. 10F, G). The reticulum on the sacci is normally prominent, but on the body, faint, and sometimes absent, at least from the proximal surface where this is seen in optical section. (Text-fig. 10F, G). All the various alternatives mentioned above can often be found within a preparation made from a single pollen sac, so that there is no question that the sundry variations in pollen form among the specimens determined as *P. africanus* indicate that more than one species of microsporophyll is present.

All but three of the specimens given separate specific names by Dr. Hamshaw Thomas are here merged with *P. africanus*. They form a series which cannot be split. As regards gross form, Dr. Thomas' specimens vary, but when my material

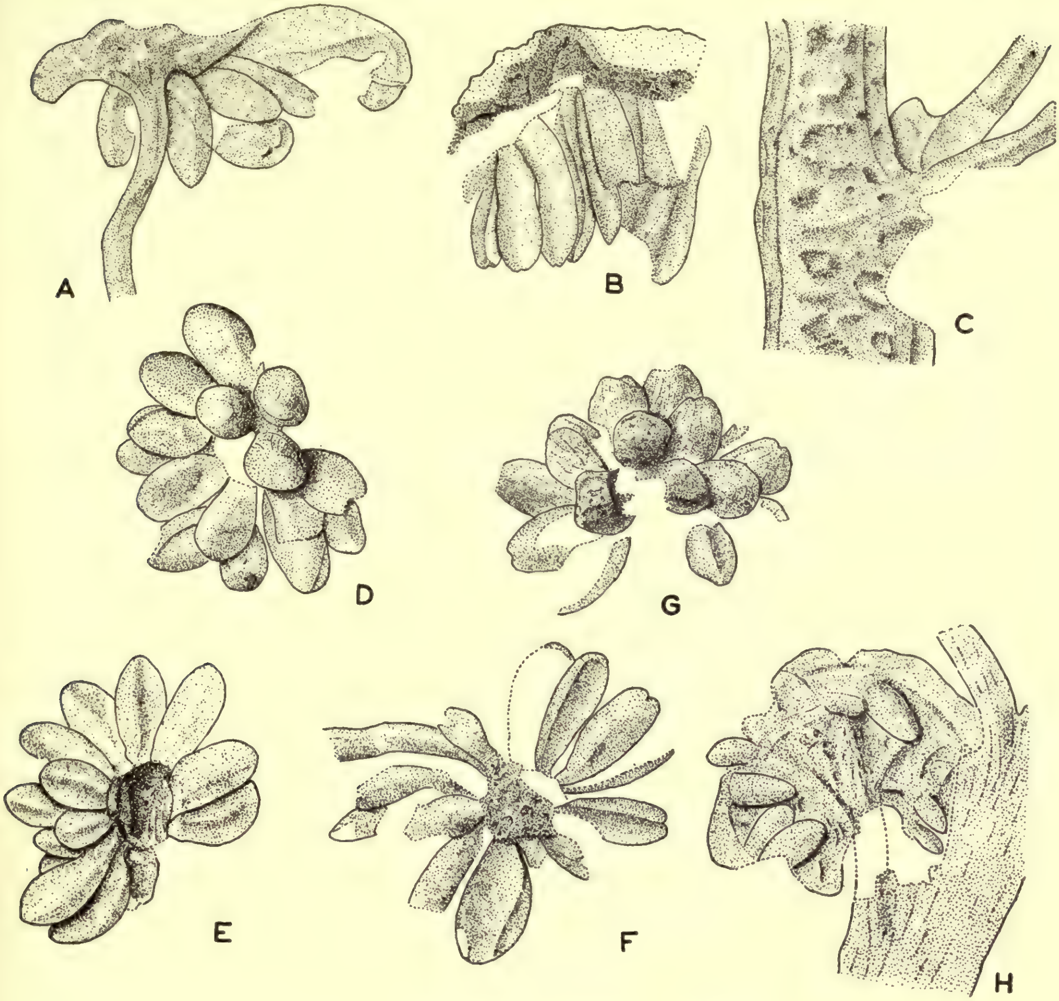

FIG. 4. *Pteruchus simmondsi, P. dubius*

A, *P. simmondsi*. Part of a sporangial head showing marginal attachment of pinna. V.42692. × 15.

B, C, *P. dubius*. B, part of a head showing slightly rugose non-sporangial surface and form of pollen sacs. V.42683. × 10. C, lowest (divided) pinna of a sporophyll, showing a pinnule set just above insertion of pinna, drawn from under side of specimen. V.42683. × 10.

D–H, *P. simmondsi*. D, E, same sporangial head before (D) and after (E) transfer, showing shape and spreading habit of pollen sacs. No marginal lobes seen. V.42693. × 10. F, G, the part (F) and transfer of counterpart (G) of a sporangial head, showing nearly smooth non-sporangial surface of head (F) and three marginal lobes (G). A fourth marginal lobe broke off in preparation. V.42687. × 10. H, sporangial head seen from sporangial surface; whole specimen seen from upper surface. It shows marginal lobes, pollen sacs vascular ridges and pinnae from this side, not interrupted by edge of rachis (cf. Fig. 2D). V.42681. × 10.

is added to his, the new specimens do not fall into his species, but fill in the gaps between them (and, indeed, extend the variation) so that the whole material forms one continuously varying series. Thomas noted the dorsiventrality of the rachis cuticle, but did not state in his cuticle figures which surface is drawn. Text-fig. 9A–D shows the cuticle from a single specimen (V.42682), it comprises very nearly all the variation seen in Thomas' figures. As already noted, the pollen points away from the suggestion that more than one species is involved. I conclude there is only one species, which is compared with the other two here recognized on p. 307, Table I.

The specimens named *Pteruchus annularioides* (pp. 297, 310) from Queensland are only doubtfully identified with *P. africanus*. The holotype is an impression only, and shows little detail (Jones & Jersey, 1947 : 55). From the existing descriptions and figures it is impossible to identify, or to reject, this species with regard to any of the better known species of *Pteruchus*. However, the figured specimens resemble small specimens of *P. africanus*, and agree in dimensions. It may be that these specimens, like the Waterfall material, are split in such a way that not all the pollen sacs are visible on any one specimen (Text-fig. 2C). Re examination of the holotype might well show that *P. annularioides* and *P. africanus* are identical ; and if so Shirley's name will have priority. While this is uncertain, however, the name *P. africanus* is provisionally retained.

The earlier records of Geinitz(1876)a and Feistmantel (1890) likewise cannot be identified, or excluded at present. When these specimens are re-examined the question of prior names will again arise. The records of Johnston (1888) and Walkom (1925) do not affect the nomenclature, since they did not give a particular name to the specimens now considered ; the leaf *Czekanowskia* (originally *Baiera*) *tenuifolia* (Johnston) Jones & Jersey (1947) is now believed to have nothing to do with *Pteruchus* (see p. 310).

Pteruchus dubius Thomas

(Pl. 24, figs. 5, 6 ; Pl. 25, fig. 3 ; Pl. 26, fig. 1 ;
Text-figs. 1E ; 4B, C ; 7B ; 8D ; 10A–C ; 11A, B)

1933 *Pteruchus dubius* Thomas, p. 241, text-figs 44, 45. Single head and part of pinna. Holotype, text-fig. 44.

1942 *Pterorrachis barrealensis* Frenguelli, p. 311, pl. 2. Large specimen, impression only.

1944 *Zuberia zuberi* Frenguelli, p. 16, pl. 2, text-fig. 12. Same specimen described. Text-fig. 12 reconstruction.

1947 *Pteruchus* cf. *africanus* Thomas : Jones & Jersey, p. 55, text-fig. 51. Impression only.

HOLOTYPE. Brit. Mus. (N.H.) No. V.23389.

MATERIAL. J. A. Townrow Colln., Nos. V.42683, V.42686, V.42695.

EMENDED DIAGNOSIS. Microsporophyll about 4 cm. long, rachis about 2·5 mm. wide at the base. About four (3–6) long, slender, often branched pinnae present. Heads elongated, from three to five times long as broad, width about 4 mm., nonsporangial surface slightly rugose, head bearing about 15 marginal lobes. Lobes small in proportion to head. Pollen sacs about 100 per head, about 2 mm. long and 1·25 mm. wide. Cell outlines faint, 1 μ wide or less, sinuosities small, normally present, 1 μ to 1·5 μ long, normally slightly pointed. Stomata more or less exposed, lateral subsidiary cells often thickened over their whole cutinized surface. Pollen with sacci normally extending on to proximal surface of grain, as long as body of grain, usually parallel-sided. Reticulum on sacci normally conspicuous, meshes about 2 μ in diameter, walls about 1 μ thick, body smooth or very nearly so. Dimensions in μ (standard deviation bracketed): Length of body 53·0 (7·35); width of body 43·3 (6·2); length of sacci 53·0 (7·05); width of sacci 33·1 (6·85); height of grain 50·0 (4·95); total width of grain 88·3 (15·3).

Description and remarks. The material includes two complete sporophylls (V.42683 V.42686; Pl. 24, fig. 5, Text-fig. 1E). Both are unforked. This species, like the others is simple and not forked. About half the pinnae are divided. In some cases this can be seen (Pl. 24, fig. 6; Text-figs. 1E, 4C and Frenguelli, 1942, pl. 2), in other cases there are more sporangial heads than pinna origins, so a division is deduced. Compressed laterally the heads are of thick substance (Pl. 24, fig. 5) and of slightly rugose surface, but much less so than in *P. africanus*. The pollen sacs are almost cylindrical, and on two small heads I counted over 100, so that this figure given in the diagnosis is probably on the conservative side; they are so crowded, however, that counting is difficult.

The cell outlines are apt to be faint, but they almost always show sinuosities. The sinuosities are larger than in the other two species (about 1·5 μ). The central part of the outlines is thin, and the sinuosities at their ends grade into the generality of the cuticle, but are distinct elsewhere, (Text-fig. 7B). The stoma in Text-fig. 8D is from a head at the top of the specimen (V.42683) where it is typical. A few, probably less than 1 in 10, are more sunken, but none so sunken as the stoma shown in Text-fig. 8B. On the lower heads the stomata may be even more exposed (Text-fig. 10). In about half the stomata seen the lateral subsidiary cells are thickened uniformly. On staining this shows as a darker area but without staining it is not visible (Text-figs. 8D, 10; Thomas, 1933, text-fig. 45).

The pollen is shown in Pl. 26, fig. 1 and Text-fig. 11A, B. The sacci overlap the proximal surface of the grain, so that they lie very nearly in the *para* position, while the body of the grain, seen in tangential longitudinal view, is higher than wide. The ornament on the sacci is usually prominent, but on the body none or almost none is visible, the proximal surface, when seen in optical section, showing at most a minutely scabrid surface. As in *P. africanus* all variants can be found in a preparation from one pollen sac.

The holotype consists of a single head, and part of a pinna. It is split through, leaving about equal proportions of plant material on both part and counterpart. Each shows part of the head and some of the pollen sacs, both of which correspond in their form with the other material here identified with *P. dubius*. However, if the part and counterpart are superimposed as they stand, because of the way the specimen is split, the pollen sacs appear to have originated all round the head (Thomas, 1933: 242, text-fig. 41). The pollen and cuticle are normal. For these reasons, I identify my material with Dr. Thomas' specimen.

The single large specimen described and figured by Frenguelli (1942, 1944) is an impression only, and there is no counterpart. Judging from the figures the specimen comprises the basal three-quarters, approximately, of the sporophyll, and there is no evidence whatever that it was forked. It is a larger specimen than any other so far discovered, but agrees with the present material in general appearance and in structure, but no cuticle or pollen is available. The specimen is therefore identified with *P. dubius*, and is included above in the synonymy of that species. I agree with Frenguelli (1942) that the other two species placed in *Pterorrachis* probably belong to different plants. The ascription of *P. dubius* to the leaf called *Zuberia zuberi* is discussed below (p. 313).

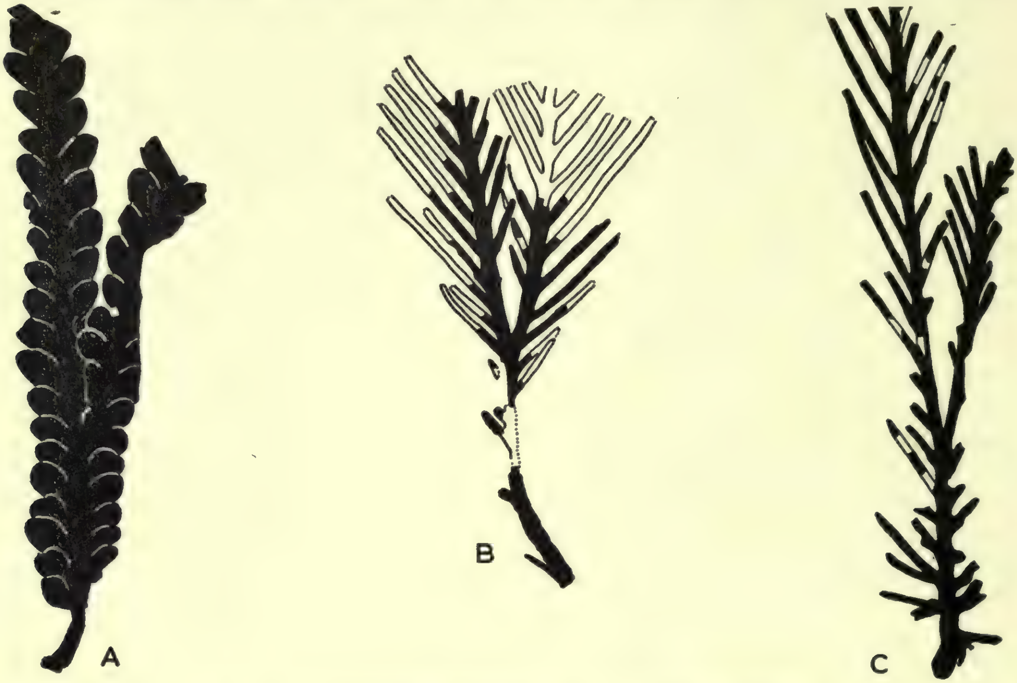

FIG. 5. *Dicroidium odontopteroides, Xylopteris elongata*

A, *D. odontopteroides*. Leaf, seen from under side, showing curving leaf base and rotated pinnae. × 1.

B, C, *X. elongata*. B, small leaf showing a small undivided basal pinnule (see also Pl. 25). × 1. C, lower portion of large leaf showing larger, divided, basal pinnule (see also Fig. 3A). × 1.

Frenguelli (1944, text-fig. 12) gives a reconstruction based on his specimen. My interpretation of the material is very different from his, and I regard his figure as misleading in most respects.

The specimen of *Pteruchus* cf. *africanus* described by Jones & Jersey (1947) is an impression, and as they remark, scarcely identifiable. However, it has divided pinnae, considerably elongated heads and small pollen sacs, and is therefore more likely to be a specimen of *P. dubius* than *P. africanus*, with which they tentatively compared it.

Pteruchus simmondsi (Shirley) Thomas

(Pl. 24, figs. 1–3 ; Pl. 26, figs. 3, 12 ; Text-figs. 2, 4, 6–8, 11)

1898 *Stachyopitys simmondsi* Shirley, p. 13, pl. 18, fig. 2. Diagnosis and fig. of holotype, but without detail. From Denmark Hill, Ipswich, Queensland. Ipswich Series.
1917 *Stachyopitys simmondsi* Shirley : Walkom, p. 13. Shirley's material, no figure.
1933 *Pteruchus simmondsi* (Shirley) Thomas, p. 233. New name only.
1944 *Stachyopitys anthoides* Frenguelli, p. 365, pls. 1, 2 ; text-fig. 1. Pl. I, fig. 3, distinct. Several specimens from Argentina.
1947 *Pteruchus simmondsi* (Shirley) : Jones & Jersey, p. 55, Shirley's material discussed. No figure.

EMENDED DIAGNOSIS. Microsporophyll about 1·5 cm. long, rachis with bulbous base. Width just above base about 1·5 mm. About 8 (4–11) short unbranched pinnae. Heads round, width from lobe to lobe about 2·5 mm. ; non-sporangial surface almost or quite smooth, substance thin, 4 (3–5) lobes per head, lobes large in proportion to head. Pollen sacs, about 15 per head, about 1·5 mm. long and 1 mm. wide. Cell outlines usually distinct, about 1·5 μ wide, straight or with small obtuse sinuosities less than 1 μ long. Stomata sunken, poles sometimes covered by terminal subsidiary cells, pit sometimes overhung by cutin flanges on lateral subsidiary cells. Pollen with sacci extending on to proximal surface of grain, parallel-sided or tapering. Reticulum on sacci conspicuous, meshes about 5 μ in diameter, walls about 1·5 μ thick ; ornament on body usually conspicuous. Dimensions in μ (standard deviations bracketed) : Length of body 58·0 (6·1) ; width of body 47·5 (4·25) ; length of sacci 55·5 (6·5) ; width of sacci 34·0 (4·05) ; height of grain 42·25 (4·35) ; total width of grain 84·5 (12·6).

HOLOTYPE. Queensland Geological Survey Colln., No. F256.

MATERIAL. J. A. Townrow Colln., Brit. Mus. (N.H.) Nos. V.42681, V.42687, V.42691–94.

DESCRIPTION AND REMARKS. The pinnae are short, compared with the size of the whole organ and no branching ones were seen ; they are alternate, but may be almost opposite (Pl. 24, fig. 3, Text-fig. 2A–C). The bulbous base is seen in the holotype (Pl. 24, fig. 2) and in two specimens from the Waterfall (Text-fig. 2A).

The marginal lobes are seldom seen complete. They may look like pollen sacs, but can be distinguished on the cuticle (p. 295). It seems that, when ripe, the pollen sacs drew away from each other, so that both they and the marginal lobes came to lie almost back to back (Text-fig. 4F). Thus in a transfer there is very little tissue of the lobes which can stick on to the balsam. Some, however, are seen in Text-fig. 4F, and others laterally compressed in Text-fig. 2A. They are large in proportion to the head, so that the whole head, when flat, has an appearance somewhat resembling a trefoil (Pl. 26, fig. 12). The head compressed laterally shows that its substance was thin and the non-sporangial surface almost or quite smooth. The pollen sacs are short and much inflated, sometimes almost globose (Text-fig. 4D).

Although the cuticle is little if any thicker than in the other species, the cell outlines are both thicker and more distinct. The small sinuosities are sharply marked off from the rest of the cuticle, being less than 1 μ long but about 2 μ wide

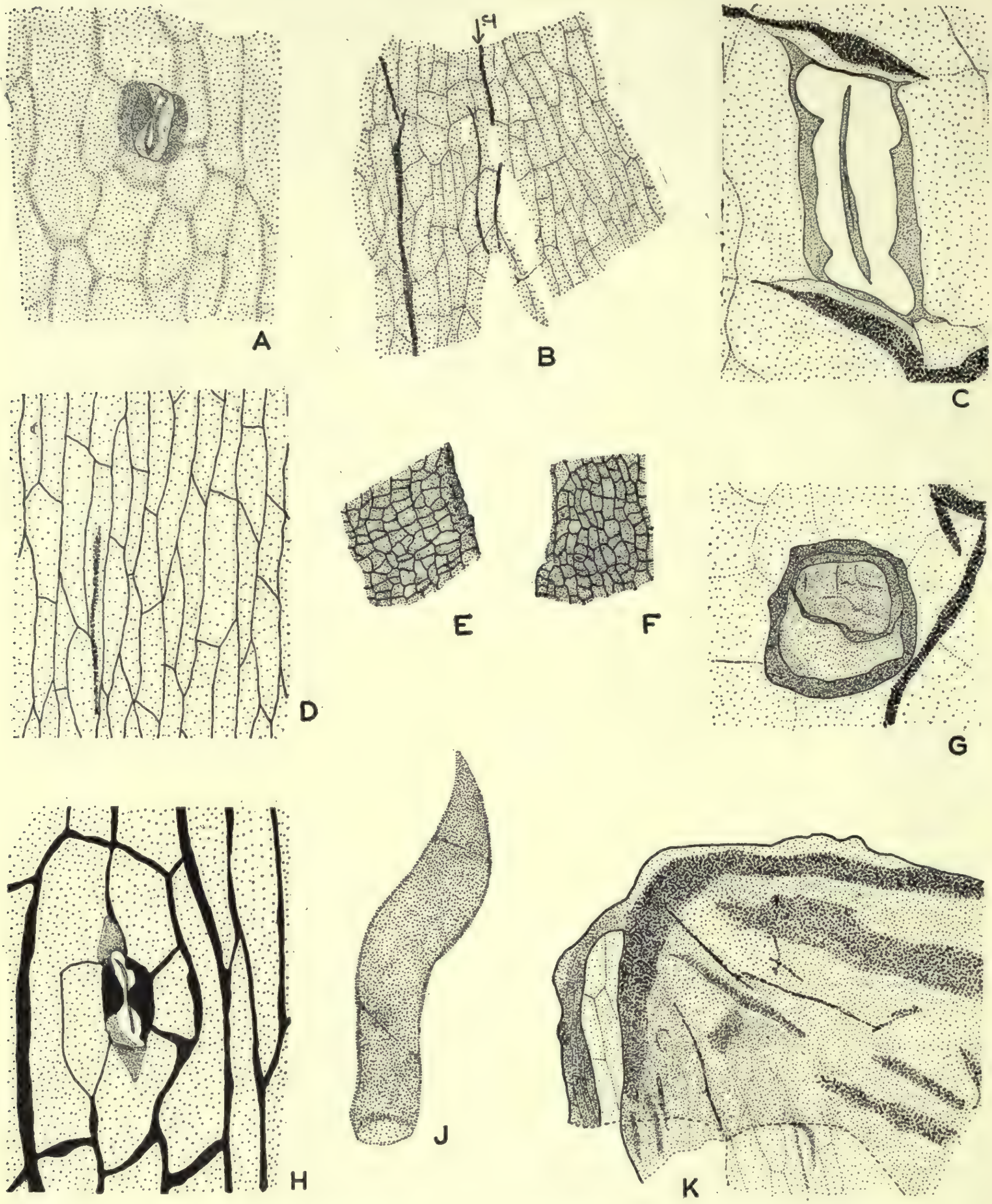

FIG. 6. A, *Phoenicopsis elongatus* ; B–D, G, *Pteruchus africanus* ; E, F, *Xylopteris elongata* ; H, *Czekanowskia tenuifolia* ; J, K, *P. simmondsi*

A, fragment from thinner cuticle (? lower) and a stoma. ×416. B, cuticle from axis, showing more or less uniform cells all over. (J) marks position where two surfaces join. V.42688. ×94. C, abnormally exposed stoma from a marginal lobe of head near base at the base the central part of the outline is wide, and with obscure edges (Text-fig. 7D). The stomata are nearly always sunken, nearly exposed ones (such as in Text-fig. 7C), probably number about 1 in 10. Text-figs. 8A, H show stomata with covered guard cell poles, and cutin flanges on the subsidiary cells. Both sorts together make up about 75% of all those seen.

The pollen is shown in Pl. 26, fig. 3 and Text-fig. 11C, D. The sacci normally overlap on to the proximal surface of the grain, but do not always, and the body of the grain in tangential longitudinal view is commonly wider than high. On the body some ornament is usually visible, sometimes a reticulum, more often irregular lines of thicker cuticle.

Thanks to the kindness of Dr. O. A. Jones, University of Queensland and of the Director, Queensland Geological Survey, to both of whom I am much indebted, I have been able to examine the holotype of *P. simmondsi* here refigured (Pl. 25, fig. 2). The specimen is an impression only, but it is identified with *P. simmondsi* because it agrees in dimensions with the present material, and because it shows the bulbous base, delicate, short pinnae and inflated pollen sacs (probably dehisced in the holotype) characteristic of this species. The impressions of the cellular outlines are very faintly seen on some of the pollen sacs ; they agree in shape and dimensions with those seen on cuticle. There are two difficulties : the pollen sacs are few, but I suspect this is connected with the way the specimen has split (cf. Text-figs. 2A–C), and one pinna on the holotype may be divided. I cannot decide whether it is, or whether we are looking at part of the sporangial head.

Frenguelli's (1944*a*) record consists of several well-preserved specimens. He does not give detail in his description, but the form and size of his specimens agree closely with mine, and so I identify his material with *P. simmondsi* ; which name therefore takes priority. The specimen figured in his pl. 1, fig. 3 shows a number of pollen sacs attached to a somewhat elongated head ; it is therefore distinct from *P. simmondsi*. It may be a small specimen of *P. africanus*, but there is not enough information for an identification.

GENERAL DISCUSSION

(1) *The Species of* Pteruchus

The three species (*P. africanus*, *P. dubius* and *P. simmondsi*) are usually distinguished readily (see Table I), but fragments may be difficult to classify, and in some species one or other character is poorly developed, and rather as in another species The specimen originally described as *Pteruchus edwardsi* Thomas is here transferred to *Stachyopitys*.

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of a sporophyll. V.42689. ×975. D, cells from cuticle of pollen sac (cf. Pl. 26). V.4269C. ×250. E, F, cuticle from opposite sides of axis, originally joined along their adjacent edges, showing more or less uniform cells all over and one stoma. From specimen figured Pl. 25. ×50. G, trichome base. V.42689. ×975. H, fragment from leaf surface with thicker cuticle (? upper) with a stoma. ×416. J, trichome from the transfer of a counterpart. V.42687. ×310. K, cuticle from apex of a pollen sac showing dehiscence slit, and in places, the cell outlines. V.42694. ×94.

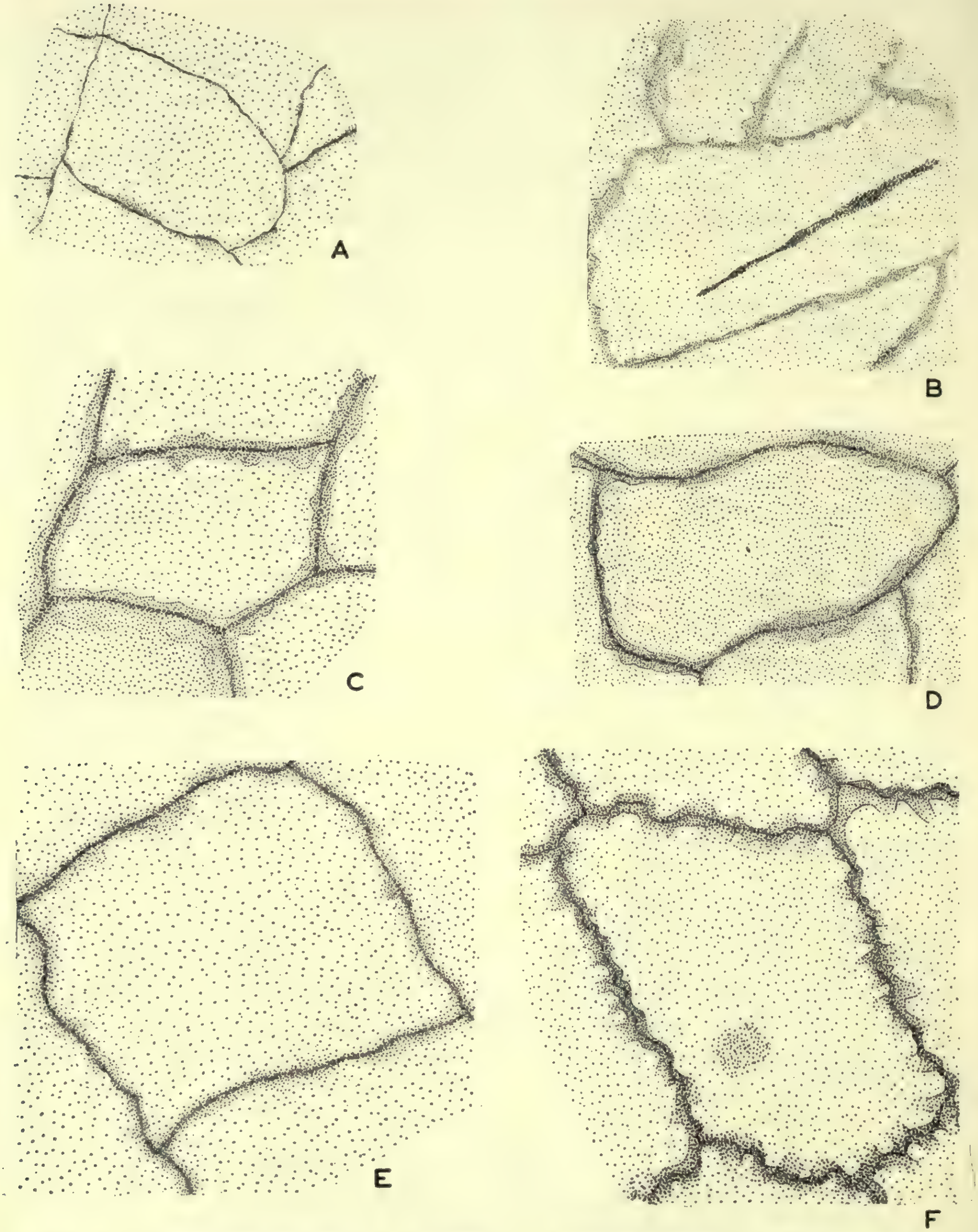

FIG. 7. A, *Pteruchus africanus* ; B, *P. dubius* ; C, *Xylopteris elongata* ; D, *P. simmondsi* ; E, *Dicroidium odontopteroides* ; F, *D. feistmanteli*

Portions of cuticle from non-sporangial surface of sporangial heads, or lower surface of lamina of leaves, showing form of cell outlines. All ×975.

Stachyopitys edwardsi (Thomas) nov. comb.

1933 *Pteruchus edwardsi* Thomas, p. 240, pl. 24, fig. 74, text-fig. 42.

I have examined the holotype (the only specimen) which is preserved as a hollow cast. It does not show much detail and lacks cuticle or pollen. I agree with Dr. Thomas that the branching is spiral, and the heads peltate with a single ring of about 8 marginal sporangia. The specimen thus differs widely from *Pteruchus* as here defined.

It bears some resemblance to *Stachyopitys preslii* Schenk (1867 : 185, pl. 64, figs. 9–12), the type species, and this genus is probably its best resting place at present (see also Seward, 1903 : 66, 67, pl. 9, fig. 2 and Gothan 1914 : 62, 63, pl. 29, fig. 4 pl. 33, fig. 3).

TABLE I.—*Comparison of the Species of* Pteruchus

	Species		
Character	*P. africanus*	*P. dubius*	*P. simmondsi*
Length . .	2·5 cm. approx.	4 cm. approx.	1·5 cm. approx.
Pinnae . .	About 5 mm. long, rarely divided	About 1 cm. long, often divided	About 3 mm. long, not divided.
Sporangial heads	Elongated to round, of thick substance, strongly rugose, *ca.* 10 lobes per head	Elongated, of thick substance, slightly rugose, *ca.* 15 lobes per head	Iso diametric, thin substance, smooth or nearly so, 3–5 lobes per head.
Pollen sacs .	More than 30 per head, about 2·5 mm. long, about twice as long as wide, slightly inflated	100 or more per head, about 2·0 mm. long, about twice as long as wide, not, or scarcely inflated	Approx. 20 per head, about 1·5 mm. long, less than twice as long as wide, markedly inflated.
Cell outlines .	Faint, about 1 μ wide, straight or slightly sinuous, sinuosities obtuse	Faint, about 1 μ wide, normally sinuous, sinuosities normally slightly pointed	Distinct, 1–2 μ wide, straight or slightly sinuous, sinuosities obtuse.
Stomata . .	Normally somewhat sunken, poles of guard cells exposed, pit not overhung	Normally exposed or slightly sunken	Normally strongly sunken, poles of guard cells sometimes covered, pit sometimes overhung by cutin flanges.
Pollen :			
(*a*) Size . .	Length *ca.* 46 μ : Total width *ca.* 63 μ	Length *ca.* 53 μ : Total width *ca.* 88 μ	Length *ca.* 58 μ : Total width 84·5 μ.
(*b*) Insertion of sacci	Not or scarcely overlapping on to proximal surface, body high as wide	Overlapping on to proximal surface, body higher than wide	Overlapping on to proximal surface, body wider than high.
(*c*) Ornament .	Obscure on body, meshes on sacci about 3 μ diameter	Body smooth or nearly so, meshes on sacci about 2 μ in diameter	Body with fairly distinct reticulate ornament, meshes on sacci about 5μ in diameter.

(2) *The Ascription of* Pteruchus *to Leaves of the* Dicroidium-Xylopteris *Group.*

(*a*) *Ascription of the Genus* Pteruchus

Thomas (1933) suggested that *Pteruchus* was the pollen organ of the leaves here called the *Dicroidium-Xylopteris* group, on account of a general similarity in cuticle, and association at the Waterfall and at one or two other localities, e.g. Denmark Hill, Ipswich, Queensland. I most fully agree. A much stronger case can now be made out than that which Dr. Thomas was able to advance.

The *Dicroidium-Xylopteris* group (see p. 288) consists of 12 or 14 extremely similar species of leaf. It is not clear whether they are best dealt with under two genera, as they are at present, or merged in one, *Dicroidium* having priority. The forking habit is common to all whilst their cuticles offer no basis for separation into different genera. It may be best to make some arbitary separation, perhaps on the number of veins at a given point in the leaf segment, but no workable distinction on such lines is yet apparent (see Jones & Jersey, 1947 : 30 for *X. tripinnata* and Townrow, 1957 : 43–45 for *D. superbum*).

Evidence for the reference of the genus *Pteruchus* to these leaves comes from agreement in anatomical structure, and from association.

(1) *Agreement in Structure*

Both leaves and microsporophylls are borne in the same way on axes that are similar, though of different sizes (p. 290, Pl. 25, figs. 2, 5). The venation of the heads of *P. africanus* at least is built upon a first division, very near the point of attachment, into three more or less equal branch veins. This is just like the venation of *Dicroidium odontopteroides*, and sometimes of *D. feistmanteli* and *D. coriacium* (Pl. 26, fig. 10 ; Text-fig. 3D, E ; Townrow, 1957 : 34, 35, text-figs 4, 9D). The cuticles of the rachises of both leaves and microsporophylls are very similar. Both show a lateral wing, both are dorsiventral by reason of the same cellular pattern, and the distribution of stomata is the same (Text-fig. 9A–D ; Townrow, 1957 : 26, text-fig. 2). As regards detailed cuticle structure, the stomata are built on exactly the same plan in both leaf and microsporophyll, being distinguishable only because the stomata of *Pteruchus* are usually smaller than on the leaves (Text-fig. 8), while both also show occasional tricellular pointed hairs of identical form (Text-fig. 6J). Other points of agreement are in the construction of the sinuosities of the cell outlines (Text-fig. 7) and in the presence of papillae (rare in *Pteruchus*) (Text-fig. 9D ; Townrow, 1957, text-figs. 5, 6).

(2) *Evidence from Association*

The genus *Pteruchus* has now been found in twelve localities, one at the Waterfall, Natal, ten in the Ipswich Series, Queensland, and one, near Ischigualasto Argentina. The position, however, is not entirely straightforward. Some of the associated leaves at the Waterfall have not yet been identified ; in the Ipswich Series (Jones & Jersey, 1947) the specimens are nearly all impressions, and only two are figured, so that there is inevitably some doubt as to the identifications ; while at Ischigualasto the complete species list is not given. For the present purpose the Ischigualasto locality is ignored (but see p. 313), all records of *Pteruchus* are treated simply as records of the genus (the species are discussed later, p. 312) and some of the most critical leaves are lumped into groups. So far as I can judge, none of these steps alters the conclusions which may be drawn.

At the Waterfall, *Pteruchus* is quite a common fossil, represented in the Townrow Collection by 51 specimens (*P. africanus* 32, *P. dubius* 5, *P. simmondsi* 14). It

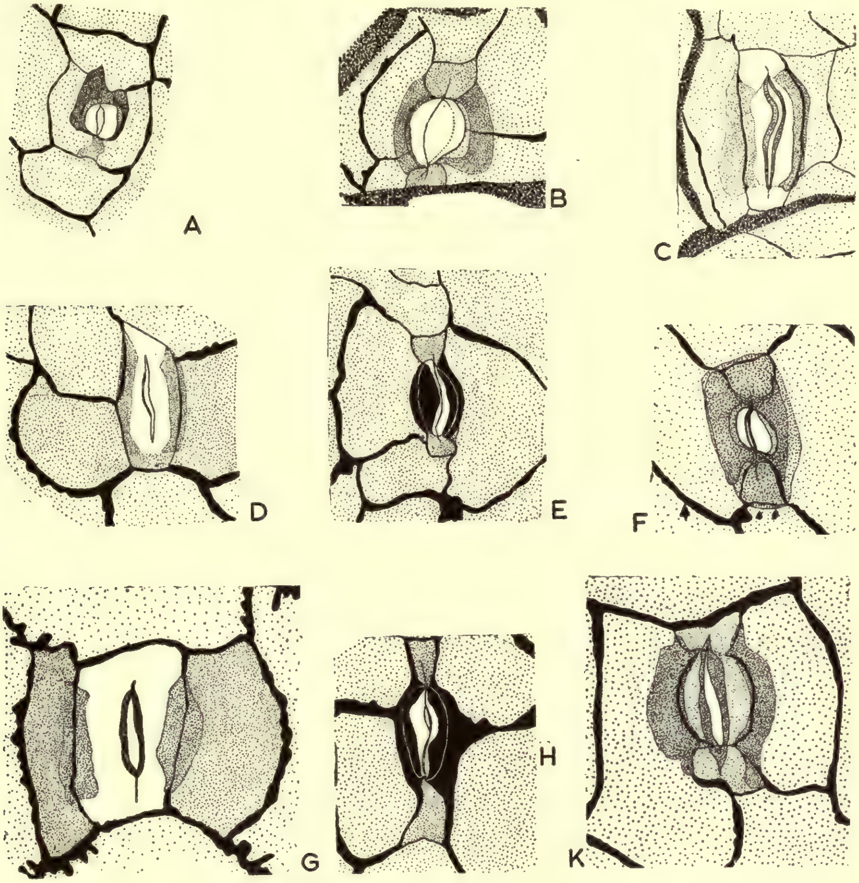

FIG. 8. *Pteruchus simmondsi*, *P. africanus*, *P. dubius*, *Dicroidium odontopteroides*, *D. feistmanteli*, *Xylopteris elongata*

A, E, *P. simmondsi*. Two stomata from same head on the same specimen showing (A) continuous cutin rim round stomatal pit, and covered guard cell poles, and (E) cutin flanges overhanging stomatal pit, and exposed guard cell poles. V.42687. B, C, *P. africanus*. Stomata from an upper (B) and a lower (C) head, each sort characteristic of the heads from which they come. V.42682. D, *P. dubius*. Stoma from a head near top of the sporophyll, of the sort most commonly met with in the species (cf. Fig. 10A). V.42683.

F, H, *X. elongata*. Comparable stomata to A and E, from under surface of same leaf. G, K, *D. feistmanteli* and *D. odontopteroides*. Stomata from the under surface of the leaves, each of the sort most commonly met with in their respective species.

All × 650.

therefore seems very probable that the leaf of the same plant is still more abundant. Only those leaves represented by more than 20 specimens are considered. Though arbitrary, this limit does include all the common fossils. The residue consists of many more rare species usually represented by 10 or fewer specimens.

Table II summarizes the facts of association of *Pteruchus*. It will be seen that (i) the three leaves *Dicroidium odontopteroides*, *D. feistmanteli* and *Xylopteris elongata* have higher scores than any other leaf, and this impression is heightened by the fact that in four out of the five localities in which *D. feistmanteli* and *X. elongata* do not occur, *D. talbragarense* and *X. spinifolia* are recorded. These leaves are exceedingly like *D. feistmanteli* and *X. elongata* and have at times been merged with them (Jones & Jersey, 1947 : 15, 28). (ii) The only other leaves which rival the above three, are *Doratophyllum tenison-woodsi* and *Czekanowskia tenuifolia* both of which are known in gross form and cuticle, and can be discussed with some confidence. (iii) No further leaves, or group, comes near the *Dicroidium-Xylopteris* group, *D. tenison-woodsi* and *C. tenuifolia* in constancy of association.

The other associates of *Pteruchus* can be excluded on their cuticles. *Doratophyllum tenison-woodsi* (Jones & Jersey, 1947 : 37, 38, pl. 10, fig. 1) has straight cell outlines and stomata surrounded by a rather regular ring of 5 or 6 subsidiary cells whose inner edges overarch and form a rim above the stomatal pit. *Czekanowskia*

TABLE II.—Pteruchus *and its Associates*

Species	Localities											Total of associations per species	Total localities 11
	Waterfall (over 20 specimens)	Ipswich Series localities (Jones & Jersey, 1944, pp. 65–71)											
		19	20	21	29	31	34	36	39	39A	Rylance No. 3 Pit		
Dicroidium odontopteroides .	+	+	+	+	+	+	+	+	+	+	+	11	
Dicroidium feistmanteli .	+	..	..	..	+	+	+	+	+	+	+	8	
Xylopteris elongata . .	+	+	+	+	+	..	+	+	+	+	..	9	
Czekanowskia tenuifolia. .	+	+	..	+	..	..	..	..	+	+	..	5	
Doratophyllum tenison-woodsi.	..	..	+	+	..	+	+	+	+	+	..	7	
Phoenicopsis elongatus . .	+	..	..	..	..	..	..	..	..	..	..	1	
? *Stachyotaxus* sp. . .	+	..	..	..	..	..	..	..	..	..	..	1	
Linguifolium lilieanum . .	+	..	..	..	..	..	..	..	..	..	..	1	
Lepidopteris stormbergensis .	+	..	..	..	..	..	..	..	..	..	..	1	
Taeniopterids (1) . . .	+	..	..	..	..	..	..	+	..	+	..	3	
Pseudoctenis, Zamites and *Pterophyllum* group (2)	+	..	..	..	..	..	..	..	+	+	..	3	

(1) Comprises the " broad leaved Taeniopterids " viz. : *T. crassinervis*, *T. lata*, *T. immersa*, *T. wianamattae*, *T. dunstani* and *T. lentriculiforme* (see Walkom, 1917 : 34–40 ; duToit, 1927 : 350–354, 401–403 ; Jones & Jersey, 1947 : 45–58).

(2) Comprises the leaves placed under *Pseudoctenis*, *Zamites* and *Pterophyllum* (in absence of information about the cuticle) by duToit, 1927 : 373–391 and Jones & Jersey, 1947 : 35–40.

In the absence of cuticle data I regard the separation of the above groups into species as nearly impossible.

tenuifolia (Jones & Jersey, 1947 : 59–61, pl. 6, fig. 2 and Text-fig. 6H) has at times been thought to be the leaf belonging with *Pteruchus* (p. 297), but its cuticle is different. It has straight cell outlines, and the stomal aperture is (at least normally) orientated parallel with the long axis of the leaf. In *Pteruchus* the stomata are (at least usually) orientated obliquely or at right angles to the long axis of the organ

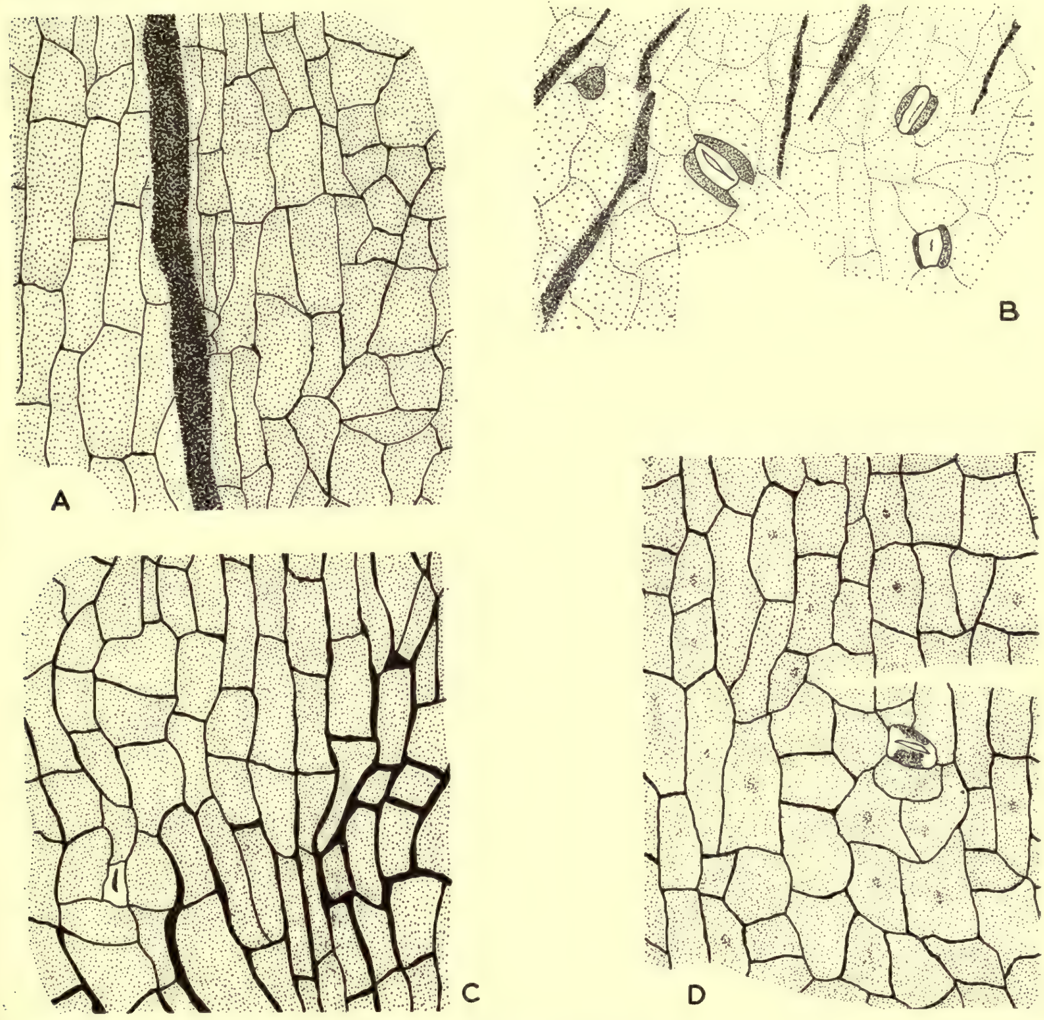

Fig. 9. *Pteruchus africanus*

A, cuticle from rachis margin (the line along which cuticle of the two surfaces joined slightly folded and shown in heavy stipple), showing elongated cells over marginal wing and different cell pattern on the two rachis surfaces (lower surface to left). B, cuticle from rachis upper surface, near top of sporophyll. C, D, two fragments of cuticle, originally opposite, from lower (C) and upper (D) rachis surfaces, showing different cell pattern on the two surfaces.

All V.42682. ×250.

on the rachis and lack any preferred orientation on the heads. The stomata of *C. tenuifolia* are normally monocyclic, but those of *Pteruchus* dicyclic. In additon the *C. tenuifolia* from the Waterfall contains dense masses (? resin) in the leaf that are resistant to maceration, but nothing like this has been found in *Pteruchus*.

Of the other associates, the *Pseudoctenis-Zamites-Pterophyllum* and the taeniopterid groups have a very thin cuticle (probably less than 0·5 μ) and so are unlikely to belong with a microsporophyll which has a thicker cuticle. The stomatal structure of these leaves is obscure, but it is less like *Pteruchus* than that of the *Dicroidium-Xylopteris* group. *Linguifolium lilieanum* (Jones & Jersey, 1947 : 48, 49) has such a delicate cuticle that I could not prepare it. *Lepidopteris stormbergensis* and *Phoenicopsis elongatus* each have stomata that are different from *Pteruchus* (Townrow, 1960 and Text-fig. 6A). The fossil called ?*Stachyotaxus* sp. (Kräusel, 1950) looks most like a conifer, and though it has stomata rather like those of *Pteruchus* it is, I think, unlikely to have anything to do with *Pteruchus*.

By the above arguments the leaves to which the three species of *Pteruchus* probably belonged are narrowed down to three, *D. odontopteroides*, *D. feistmanteli* and *X. elongata*.

It is not yet possible to say with much conviction which species of *Pteruchus* belongs with which leaf ; the cuticles are too alike, and evidence from association is still slight. There are, however, small cuticle differences which suggest that *D. odontopteroides* and *P. africanus* (the commonest leaf and sporophyll), *D. feistmanteli* and *P. dubius* (the rarest) and *X. elongata* and *P. simmondsi* (intermediate as regards abundance) belong together. This suggestion is based on a comparison of cuticle of lamina and sporangial head. The cuticle of the rachises is nearly indistinguishable in both leaves and sporophylls, it lacks the distinctive form of the cell outines and shows stomata often of somewhat anomalous form and degree of sinking.

In *D. odontopteroides* the central part of the cell outline is thin, but distinct, and the small sinuosities tend to grade into the general cuticle so gradually that their exact outline is hard to see. In *D. feistmanteli* the central part of the outlines is thin but distinct and the sinuosities are large, and distinct for most of their margins. In *X. elongata* the central part of the outline is wide but with indistinct edges, while the small sinuosities are clearly marked off from the rest of the cuticle. The three species of *Pteruchus* show similar differences (Text-fig. 7).

In *D. odontopteroides* the stomata are normally sunken, but the stomatal pit is not overhung and the guard-cell poles exposed : the same is true of *P. africanus* (p. 298, Text-fig. 8B, C, K ; Townrow, 1957, text-fig. 6). In *D. feistmanteli* and *P. dubius* the stomata are, at most, only slightly sunken, while there is a general thickening of the lateral subsidiary cells in about half the stomata seen (p. 297, Text-fig. 8D, G ; Thomas, 1933, text-fig. 45 ; Townrow, 1957, text-fig. 9). In such specimens of *X. elongata* as I have examined and in those which have been adequately figured, the stomata are sunken and are either overhung by cutin flanges borne on the lateral subsidiary cells, or by a continuous cutinized margin of all the subsidiary cells, so that the guard cell poles (though partly cutinized) are covered. In *P. simmondsi* stomata with these features represent about three-quarters of all those seen (p. 305, Text-fig. 8A, E, F, H ; Jones & Jersey, 1947, pl. 3, fig. 1).

However, the differences discussed above are slight and subject to variation (see p. 295); they cannot sustain the weight of much argument. It seems likely that evidence from repeated association is necessary before reference of leaf to sporophyll at specific level can be made convincing.

Frenguelli (1944) regarded the microsporophyll he called *Pterorrachis barrealensis* (here *Pteruchus dubius*, p. 300), as belonging with the leaf he calls *Zuberia zuberi*. The evidence is restricted to the association of a single sporophyll with the leaves. The leaf called *Z. zuberi* is composite. Frenguelli has ignored cuticle data, but some of his figures show the thick leaf substance which is characteristic of the genus *Hoegia* and distinguishes it at once from *Dicroidium* (Frenguelli, 1944, pl. 9, figs. 1, 2; ? pl. 7, fig. 3): other figures are indistinguishable from *Dicroidium feistmanteli* (pls. 1, 4 & ?8, fig. 4). Others again are indeterminable on the information given. I accept the reference of Frenguelli's specimen to *Dicroidium feistmanteli*, but it is most unlikely that *Hoegia* has anything to do with *Pteruchus* or *Dicroidium*. It has a very thick leaf substance and a thick cuticle quite different from *Pteruchus* (Townrow, 1957 : 47–51).

Frenguelli (1944*a*) records that the fossil he named *Stachyopitys anthoides* (here *P. simmondsi*) was found in a locality in the Estratos de Potrerillos where *X. elongata*, *Equisetites* and *Yabeiellia* spp. were common; but *D. odontopteroides* and *D. feistmanteli* are not mentioned. This may be additional evidence from association that *P. simmondsi* belongs with the leaf *X. elongata*, as is suggested on other grounds above (p. 312).

(3) *The Morphology of* Pteruchus

Thomas (1933 : 265; 1933*a* : 31, 40) has suggested that *Pteruchus* was a sporophyll, but by using the terms " axis ", " bract " and " branch " (here rachis, pinnule and pinna) kept open the possibility that it was of stem-like nature, or a combination of leaf and stem. More evidence is now to hand, and I conclude that *Pteruchus* is best regarded purely as a sporophyll; i.e. that it is of leaf-like nature, and not like any other category of organ.

Pteruchus africanus is known to be borne directly on a stem in the manner of a leaf, and not in the axil of a leaf or bract (p. 292).

All three species show characters that are normal in leaves but not normal in stems, namely (1) They are built upon a pinnate plan throughout (pp. 290, 294); (2) they are dorsiventral and bilaterally symmetrical (pp. 290, 294); (3) the pinnae are offset towards the upper surface of the rachis like many (probably most) compound leaves, and certainly like the leaves *Dicroidium* and *Xylopteris* (Text-fig. 3D, E; Townrow, 1957 : 28).

In two features the microsporophylls resemble the leaves to which they are referred but differ from the axes of the same plants: (1) the rachis cuticle is dorsiventral in microsporophyll and leaf, but is similar all over the axes (Text-fig. 6B, E, F); (2) the rachises of leaf and microsporophyll have a lateral wing, absent from the axes (p. 292).

The structures here called pinnules, but referred to as bracts or bracteoles by Thomas were what caused him to suggest that *Pteruchus* might possibly be of stem-

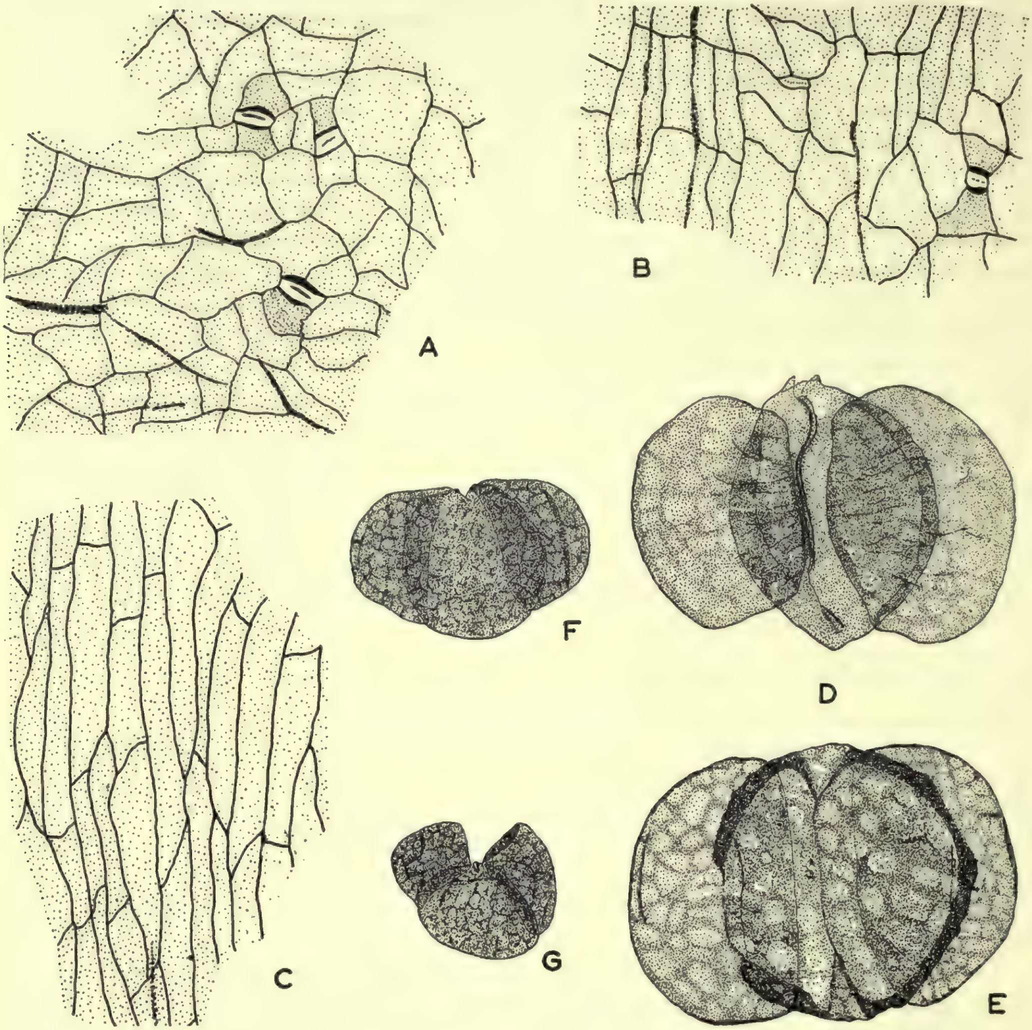

Fig. 10. *Pteruchus dubius*, *P. africanus*

A–C, *P. dubius*. A, cuticle from non-sporangial surface of head showing pattern of cells and stomata. V.42695. ×250. B, C, cuticle fragments originally opposite, from upper (B) and lower (C) surfaces of rachis, showing difference in cell pattern and usual orientation of stomata. V.42695. ×250. D–G, *P. africanus*. D, E, two pollen grains in distal (D) and proximal (E) polar views, showing sulcus and variation in shape and ornament of body and sacci. From same sporophyll, but not same pollen sac. V.42689. ×975. F, G, two pollen grains in tangential longitudinal view showing sulcus and variation of position of insertion of sacci. From the same pollen sac. V.42688. ×525.

like nature. The question is whether these organs are more like pinnules of a pinnate leaf, or bracts on an inflorescence. The reasons why they seem to me to be like pinnules and not bracts are as follows: (1) They are only produced occasionally, as might be expected of lower pinnules; but morphologically important organs like subtending bracts, or even bracteoles, should be constant. (2) No specimen has been seen which subtended a pinna, (or branch as it might be). (3) The pinnules set near the base of the microsporophyll have close agreement with a basal pinnule sometimes produced by leaves of the *Dicroidium-Xylopteris* group (Text-figs. 2A, B, 5B, C). (4) The two alternately arranged pinnules near the sporophyll base in V.23360 (Text-fig. 3B) can easily be explained as reduced alternate pinnae; to regard them as bracteoles involves a number of assumptions (e.g. that the organ here called a sporophyll is part of a larger organ that has never been seen complete) which run contrary to other evidence, and have nothing to support them.

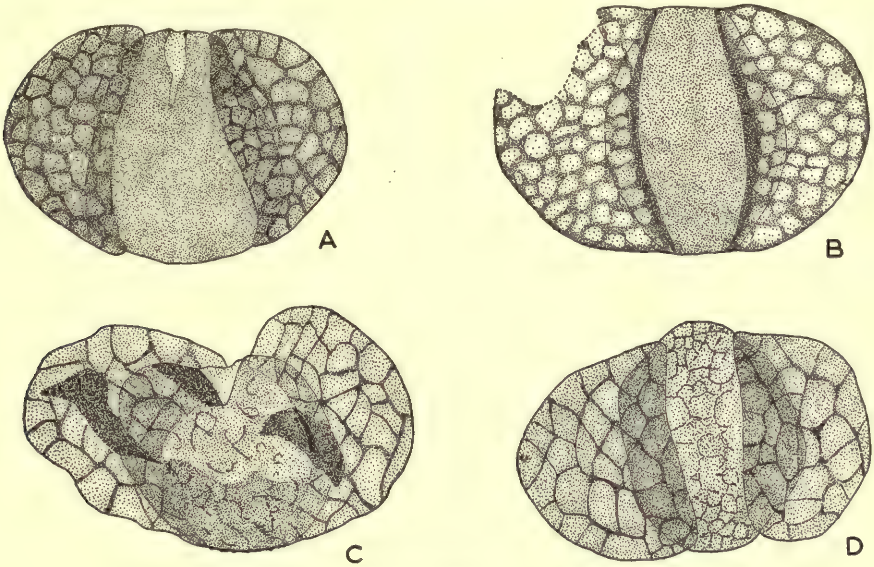

FIG. 11. *Pteruchus dubius, P. simmondsi*

A, B, *P. dubius*. C, D, *P. simmondsi*. Pollen grains in lateral (A, C) and proximal (B, D) polar views, showing body shape, insertion and ornament of sacci. A, B, holotype, V.23389. C, D, V.42694. All ×650.

On the other hand, I can find no evidence that suggests that *Pteruchus* is a stem-like structure. Regarded as a sporophyll all the available evidence falls into a coherent picture; but regarded as any other sort of organ a number of points cannot be made to fit in, and must be dismissed arbitrarily as of no importance (Thomas, 1933: 200).

Regarded as a sporophyll, the nature of the sporangial heads is easily explained. They are the distal portions of the pinnae, expanded into a lamina, bearing sori along the veins, the sori lacking a definite boundary, and becoming concrescent towards the centre of the head. They are thus analagous to the sori of e.g. *Acrostichum aureum*. This view avoids the more complicated explanations, involving the possible presence of a cupule (an organ never satisfactorily defined, and of uncertain morphology) into which Thomas (1933 : 265) was obliged to enter.

At present I express no views upon possible homologies between the parts of *Pteruchus* and of *Umkomasia* and its allies, though, like Thomas, I believe they belonged to the same plants.

(4) *Comparisons and Taxonomic Position*

A full discussion of the taxonomic position of the Corystospermaceae must wait until their seed-bearing organs are reconsidered. At present *Pteruchus* is compared with various other pollen organs to clear the ground for such a wider discussion. Here the older and usually more inclusive terms Pteridospermae (= Cycadofilicales), Lyginopterideae, Medulloseae and Corystospermaceae are used in preference to any of the more recent alternatives (Pant, 1957). This is for two reasons. The first is that for the present purpose, the older terms are more useful. The second is that the fundamental point—the morphology of the seed-bearing organs of the Corystospermaceae—is not yet satisfactorily decided. Thomas (1933 : 256) describes them as inflorescences, but points out several facts inconsistent with this view : until these organs are re-examined and their morphology decided, the Corystospermaceae cannot be classified otherwise than as a family *incertae sedis*.

A difficult point in comparing *Pteruchus* is that there is no evidence suggesting which way evolution within the genus has gone. Taking different basic premises any of the species could be called the most primitive, and the others derived from it, or all could be considered equally advanced, derived independently from a common (hypothetical) ancestor. Accepting the suggested ascriptions to the leaves (pp. 312, 313) it is not clear which is the older (Jones, 1949 ; Jones & Jersey, 1947 : 73), hence this line of argument does not help.

Thomas regarded the Corystospermaceae as belonging to the Pteridospermae. I agree entirely, if we define the Pteridospermae as " gymnospermous plants with leaves, pollen- and seed-bearing organs pinnate. Reproductive structures not aggregated in cones or flowers ".

Pteruchus has been compared with *Crossotheca* (Kidston, 1923 ; Remy, 1956) by Thomas (1933 : 256). They are alike in two respects : both are pinnate and bear the pollen sacs on what is most reasonably regarded as a modified pinna or pinnule. Otherwise they are different ; differing in the manner of insertion of the pinna petiole, the way in which the pollen sacs are arranged, and in that *Crossotheca* (at least the better known species) has bilocular synangia. *Crossotheca* is regarded as belonging to a lyginopterid plant (Jongmans, 1950).

There is some resemblance between *Pteruchus* and *Potoniea* (Halle, 1933 ; Remy, 1956) for both bear long, free, unilocular sporangia, dehiscing by a longitudinal slit, toward the centre of a cup-like pinnule with a lobed or dentate margin. *Potoniea* is attached basally, and the pollen differs.

Thomas (1933 : 254) also compared *Pteruchus* with *Dictyothalamus schrollianus* W. & R. Remy, 1958). There are a number of most interesting similarities. *D.*

schrollianus is pinnate, and may be forked, and the rachis is lumpy, at any rate in some specimens, like *Pteruchus*. The pollen sacs are massed over one surface of the " head ", and the pinna appears to be inserted on, or mostly on, the sporangial side, and its continuation on to the " head " is free of pollen sacs. The pollen sacs probably lie in rows, as may be so in *Pteruchus*. The comparison cannot be pressed too far. The pollen of *D. schrollianus* is monosaccate, while the structure of the " head " and pollen sac is unknown. *D. schrollianus* is of unknown affinities. Its pollen is like that of *Schuetzia anomala* (Remy & Rettschlag, 1954 ; W. & R. Remy, 1958) but otherwise the two organs appear to be rather different.

Two Rothliegend fossils, *Pteridospermostrobus gimmianus* Remy (1954) and *Manebachia polysporangiata* W. & R. Remy (1958*a*) bear superficial resemblance to *P. simmondsi* and *P. dubius*, but differ in structure. *Thuringia callipteroides* Remy (1953) has bisaccate pollen like *Pteruchus* but is otherwise quite different. According to Potonié & Kremp (1956) the pollen of *T. callipteroides* is monosaccate, however.

Pteruchus shows no point of approach to any Medullosean pollen organ (Halle, 1933), neither is it like any of the fructifications belonging to *Glossopteris* and *Gangamopteris* (Plumstead, 1959, discussion). It differs widely from those fossils found associated with *Glossopteris* (Thomas, 1958 ; Pant, 1958), except that it has bisaccate pollen.

There are no Mesozoic fossils that can be closely compared with *Pteruchus*. Among the supposed pteridosperm derivatives *Caytonanthus* (Harris, 1950, discussion) is pinnate and has bisaccate pollen like *Pteruchus*. *Caytonanthus* bears a radially symmetrical group of (usually) four pollen sacs, pendulous from an unexpanded branchlet end of the sporophyll, which dehisces by the pollen sacs splitting apart from one another. These features are quite different from anything seen in *Pteruchus*, and, in detail the pollen is different ; *Caytonanthus* pollen is about 15 μ wide, and has a scarcely visible sulcus, but *Pteruchus* pollen is about 70 μ wide, and shows a distinct sulcus.

Antevsia the pollen organ of the Peltaspermaceae (Townrow, 1960) resembles *Pteruchus* only in being pinnate and in having pollen sacs that dehisce by a longitudinal slit. Otherwise it differs markedly. The pollen sacs are either borne marginally on a disc, or on the under surface, possibly opposite on marginal lobes, of a fertile branchlet of the sporophyll. The pollen sacs are massive, with stomata, and probably with vascular tissue. The pollen is monosulcate.

Four other Triassic fossils have bisaccate pollen rather like *Pteruchus*. They are : *Harrisiothecium marsiloides* (Harris, 1935 ; Lundblad, 1950) which branches in all three planes, and has a two-valved synangial pollen-bearing portion with immersed pollen sacs, one row in the tissue of each valve. It is thus widely different from *Pteruchus*. *Pamelreuthia halberfelneri* (Kräusel, 1948) which is pinnate, but differs in having pollen sacs, probably one row, sunken in the tissue of the expanded pinna ends, so forming synangia. *Ruhleostachys pseudoarticulatus* Roselt (1956) which is an organ of entirely different structure from *Pteruchus*, probably very close to the conifers, and the conifer *Voltzia* (?) *heterophylla* (Wills, 1910 ; Couper, 1958), which is clearly unconnected with *Pteruchus*.

It has been suggested (Thomas, 1933 : 260) that *Pteruchus* is comparable with a catkin, e.g. of *Populus*, but since *Pteruchus* is a sporophyll this comparison cannot be maintained.

In conclusion, the genus *Pteruchus* cannot be exactly classified. It resembles a number of fossils in being pinnate, or having bisaccate pollen, or pollen sacs that dehisce by a longitudinal slit ; but these are all characters which are shared by a wide range of plants otherwise dissimilar. The bisaccate pollens, for example, are very numerous and all rather similar (see Potonié, 1958). As far as evidence from the pollen organs goes, *Pteruchus* is remote from any of the " Mesozoic Pteridosperms " (including, for convenience only, the Caytoniales), indeed, as far as they are known, each of the " Mesozoic Pteridosperms " is remote from the others. The evidence (and it is far from complete) suggests that they are so different that they are best placed in different orders (but see Gothan & Weyland, 1954). Among the Palaeozoic pteridosperms comparison is possible, though never close, between *Pteruchus* and pollen organs in which the pollen sacs were borne on a laterally attached pinnule. This seems to have been a character of the Upper Carboniferous Lyginopterideae (if indeed *Crossotheca* did belong to a lyginopterid plant), and so suggests some connection with the Lyginopterideae. The differences between *Pteruchus* and any lyginopterid fossil indicate the connection is remote.

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PLATE 24

Pteruchus simmondsi (Shirley)

FIG. 1. A sporophyll showing alternate branching. V.42681. ×2.

FIG. 2. The holotype. Queensland Geological Survey No. F.256. ×2.

FIG. 3. The lower portion of the sporophyll shown in Fig. 1, showing form of sporangial heads and of the pinnae. ×6.

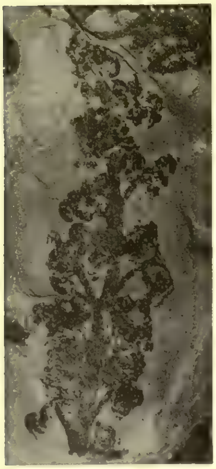
Pteruchus africanus Thomas

FIG. 4. A sporophyll (in transfer) seen from the upper surface. V.42682. ×2.

Pteruchus dubius Thomas

FIG. 5. A sporophyll. V.42683. ×2.

FIG. 6. Base of the same specimen, showing basal pinnule (right), ? fragment of axis (left) and first pinna with pinnule just above its insertion (cf. Text-fig. 4c). ×7.



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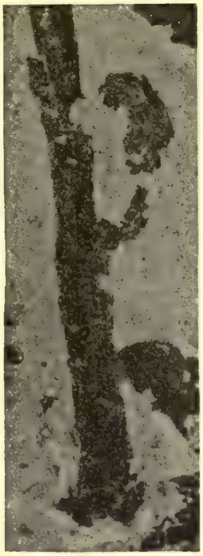

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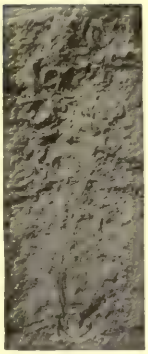

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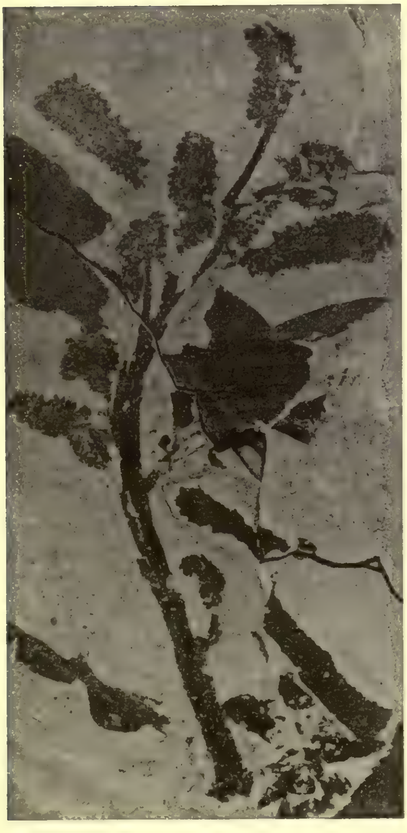

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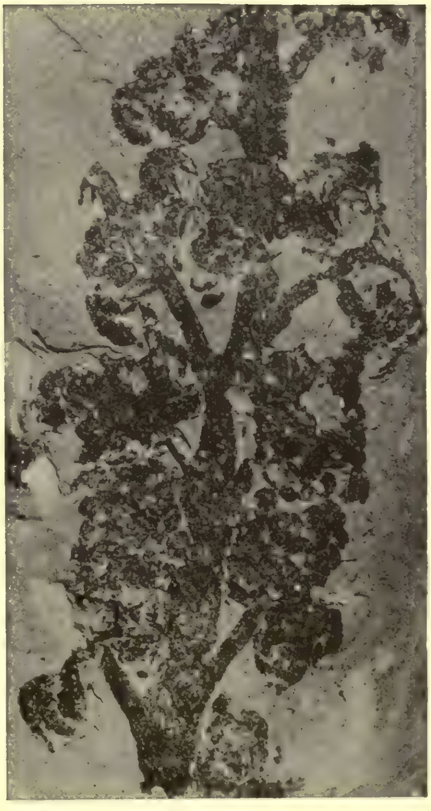

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PLATE 25

Pteruchus africanus Thomas

FIG. 1. Lower portion of a sporophyll showing single pinnule about midway between sporophyll base and first pinna. V.42684. ×6.

FIG. 2. Portion of axis (horizontal) and base of a sporophyll (curving to run vertically). Photograph taken under NH_4Cl; illuminated from bottom left. V.42685. ×6.

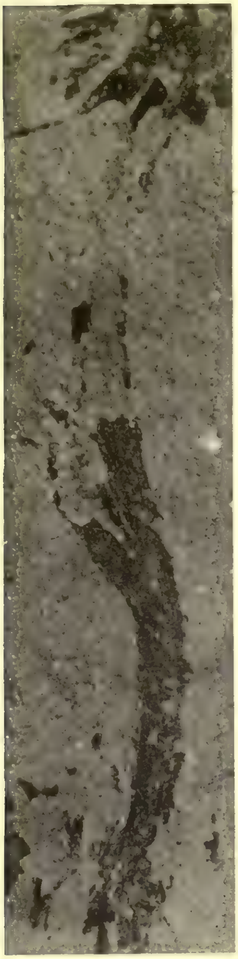
Pteruchus dubius Thomas

FIG. 3. A sporangial head, sporangial surface exposed, showing insertion of pinna, marginal lobes devoid of pollen sacs (next pinna insertion and at distal end) and pollen sacs over rest of the surface. V.42686. ×6.

Xylopteris elongata (Carruthers)

FIG. 4. The base of a leaf showing long but undivided basal pinnule (cf. Text-fig. 5B). ×6.

FIG. 5. A leaf base attached to a short piece of axis (running to right). ×6.



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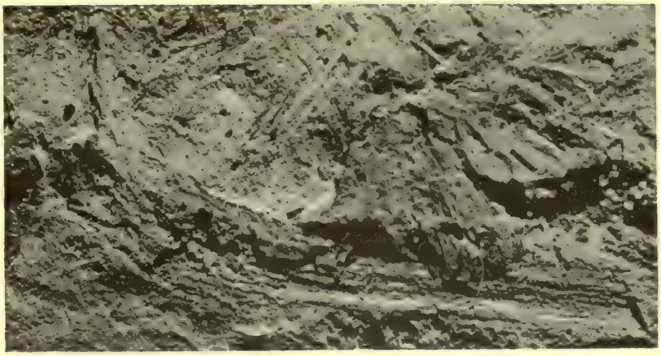

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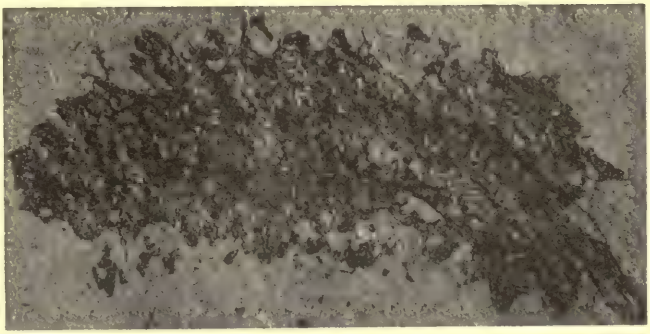

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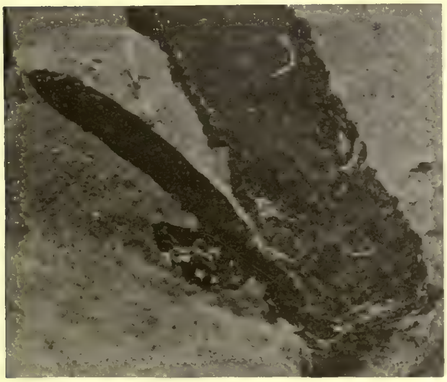

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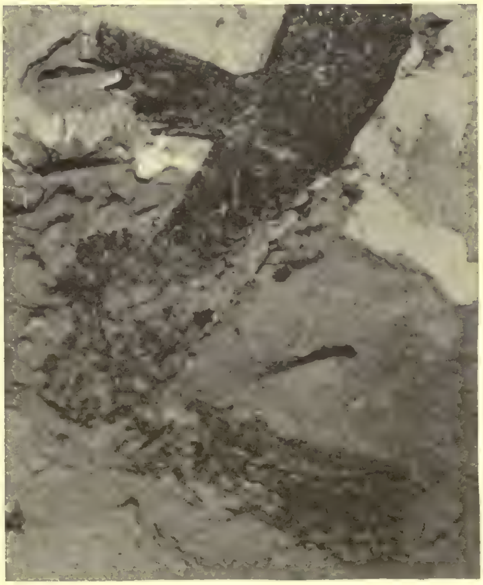

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PLATE 26

Pteruchus dubius Thomas

FIG. 1. Pollen grain, polar view distal face, showing sulcus. An abnormally small specimen. V.23389. ×500.

Pteruchus africanus Thomas

FIG. 2. Pollen grain, tangential longitudinal view, showing sulcus in optical section and insertion of sacci. V.23384. ×500.

FIG. 4. Pollen grain, polar view distal face, showing sulcus. V.23384. ×500.

FIG. 5. Section of a pollen sac showing single loculus. V. 42688. ×260.

FIG. 6. Sporophyll base showing a single pinnule and an impression of another or (?) of part of the axis. V.23385. ×9.

FIG. 7. The cuticle of the edge of a head showing small foldings and cuticle extending as a rim on to sporangial surface (at *a*).

FIG. 8. A head, showing the rugose (non-sporangial) surface. V.42682. ×7.

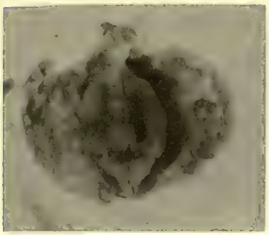
FIGS. 9, 10. Two heads, sporangial surface seen free of pollen sacs, showing area of pollen sac attachment, and ridges marking course of veins. Note margin and lobes smooth, and in Fig. 9 little rings running more or less parallel with a vein. Photographs taken under NH_4Cl, illuminated from bottom left. V.23394. ×7.

FIG. 11. Part of pollen sac wall (in transfer) showing single layer of cells forming the wall at maturity. V.42690. ×50.

Pteruchus simmondsi (Shirley)

FIG. 3. Pollen grain, polar view distal face, showing sulcus. V.42687. ×500.

FIG. 12. A head, sporangial surface exposed, showing pinna insertion and large marginal lobes. V.42681. ×7.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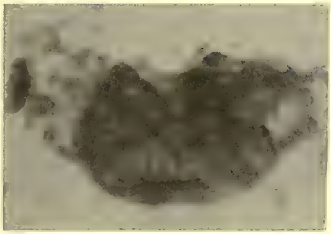
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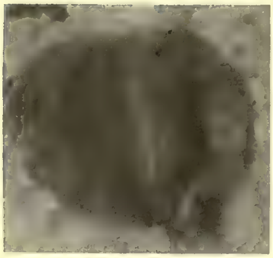
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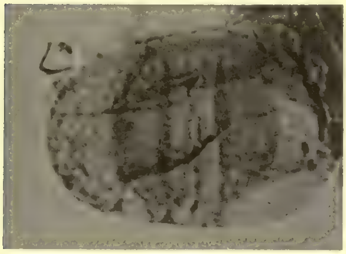
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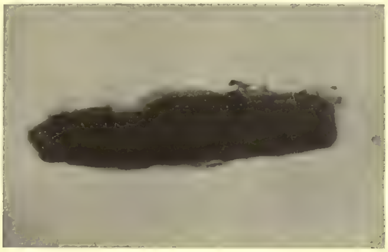
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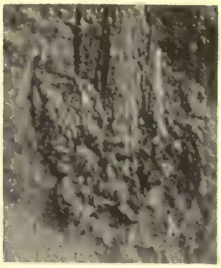
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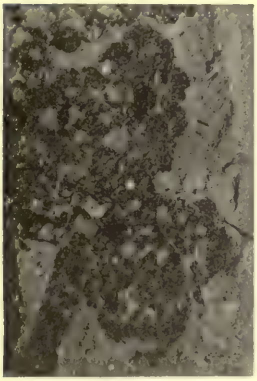
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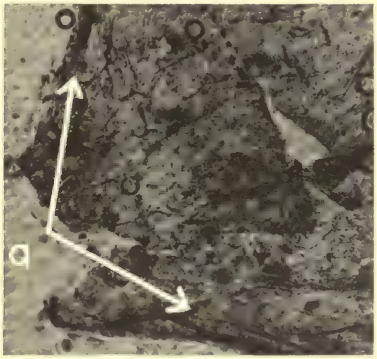

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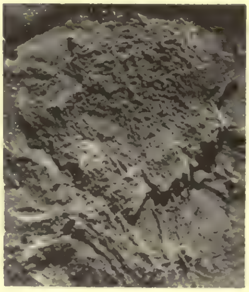
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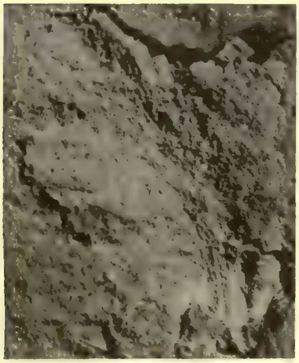
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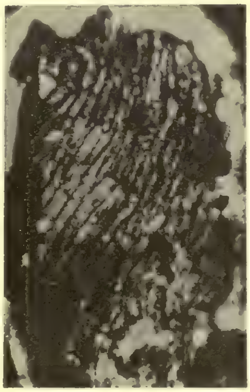
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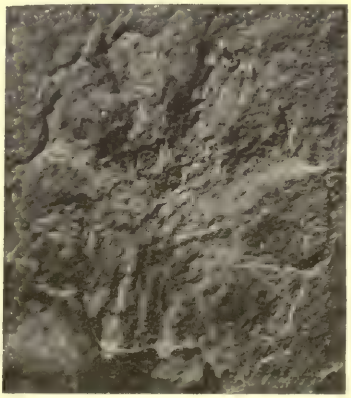
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REVISION OF THE OLIGOCENE FLORAS OF THE ISLE OF WIGHT

BRITISH MUSEUM
1 FEB 1963
NATURAL HISTORY

M. E. J. CHANDLER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 6 No. 3
LONDON: 1963

REVISION OF THE OLIGOCENE FLORAS OF THE ISLE OF WIGHT

BY

MARJORIE E. J. CHANDLER

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Pp. 321–384 ; *Pls.* 27–35; 5 *Text-figures*

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REVISION OF THE OLIGOCENE FLORAS OF THE ISLE OF WIGHT

By M. E. J. CHANDLER

SYNOPSIS

The beds from which plant remains have been obtained are listed ranging from the base of the Upper Headon to the top of the Hamstead Series. Reasons for excluding the Lower Headon from the Oligocene are briefly summarized. The poor representation of the Oligocene land flora in the Isle of Wight is mentioned and the plant beds of the successive horizons, Upper Headon, Osborne, Bembridge and Hamstead are described. Plant lists from these beds are incorporated and are discussed in turn. In the systematic section almost all the records in the Upper Headon are new as are the few from the Osborne Beds. In the Bembridge Series there is a small collection of plants to add from the Bembridge Limestone and a few new plant localities in the Bembridge Marls. There are one or two corrections to the plant lists from the Insect Limestone published in 1926 but this flora is due shortly for reappraisal. The Hamstead Bed flora is still little known and is represented almost entirely by water or marsh plants which give the minimum of information about contemporary conditions.

INTRODUCTION

THE horizons from which plant remains have been collected in the Oligocene Beds of the Isle of Wight are, passing downwards,

The Hamstead Beds,
The Bembridge Beds, especially the Insect Limestone,
The Osborne Beds where only sparse dwarfed or battered specimens have been found,
The Upper Headon Beds.

The plants will be discussed chronologically starting at the Upper Headon and working up through successive horizons.

The Eocene plants, very few in number in the Island, have been described elsewhere except for the Alum Bay pipe-clay impressions which have not been revised in recent years so that a thorough study of the remains, mostly leaves, is needed but must await the attention of an expert in these organs. Unfortunately the macroscopic plant remains do not, at present at least, appear to help in the separation of Eocene and Oligocene.

Whereas some geologists include the Lower Headon Beds in the Oligocene (Reid & Strahan, 1889 : 127 ; Arkell, 1947 : 217) others have preferred to retain them in the Eocene (Wrigley & Davis, 1937 : 220, pl. 18). The latter position was adopted by Chandler (1961, table on p. 8). In the type localities of the Barton and Hordle cliffs there is a continuous section from the Barton Beds through passage beds into the Lower Headon while the succeeding Marine Beds (if indeed they represent the Middle

Headon Marine Series) are ill-developed. There are no Upper Headon strata. In the Isle of Wight the Upper Headon Beds are definitely and unmistakably separated from the Lower Headon by the well-developed marine Middle Headon with its " Venus " and *Neritina* Beds and Oyster banks, and the division between Eocene and Oligocene appears to be drawn more appropriately below these marine beds with Lattorfian mollusca than below the Lower Headon.

RESTRICTED RANGE OF PLANT REMAINS AVAILABLE UP TO THE PRESENT

The Oligocene plant remains of the Isle of Wight are disappointing after the relatively richer beds of the Eocene on the Mainland. Apart from the fine impressions of Bembridge age in the Insect Limestone at Thorness and Gurnard Bays (Reid & Chandler, 1926) very little evidence of the true land flora is preserved. The frequent mention of seed beds at a number of horizons in the Geological Survey Memoirs has in the past raised false hopes in the palaeobotanist for these invariably prove to be monotonous bands of gregarious water plants : *Stratiotes*, *Brasenia* and *Limnocarpus* with a limited representation of other genera like *Potamogeton*, *Aldrovanda* and *Typha*. There are in addition occasional finds in the Hamstead Beds of *Sequoia couttsiae* represented either by carbonaceous twigs or by hollow impressions in cementstone or ironstone blocks. No one has yet discovered lenticles or pockets rich in the fruits and seeds shed by trees and shrubs clothing the banks of rivers or growing in woodlands adjoining them, although search has been made for such by numbers of workers including C. Reid, J. Groves, G. W. Colenutt, E. M. Reid and M. E. J. Chandler. No typical patches dark with the remains of twigs and woody fruits have been observed. The nearest approach to such is a sandy band below a sewer pipe at Linstone Chine, Colwell Bay, where scattered fruits are easily removed from soft sands by sifting. That it may be worthwhile to continue to search is suggested by the unique but important find in a thin seam composed of tiny shreds of vegetation in the Upper Headon of Colwell Bay of *Anemia colwellensis* and of distinctive leaf fragments described as an unknown leaf. (p. 357).

CHRONOLOGICAL REVIEW OF PLANT-BEARING BEDS AND LISTS OF ASSOCIATED PLANTS

(a) *The Upper Headon Beds*

All the plants hitherto found come from Colwell Bay where the beds present a very variable series of brown, green, greyish or variegated clays with some white sands and impure limestones. They are brackish, estuarine and freshwater deposits with an abundance of shells displaying the paucity of genera and species usual under such conditions coupled with an abundance of individuals. Among the genera are *Paludina*, *Potamomya*, *Cyrena*, *Melania*, *Limnaea*, *Potamides* and *Planorbis* (names used in the Survey Memoir now in some cases superseded). An excellent description of the section was given by Keeping & Tawney (1881) while a typical section in Colwell and Totland Bays is given in Reid & Strahan (1889 : 131). This locality does not show the massive limestones found at Headon Hill (see Reid & Strahan, 1889 : 129), but from the point of view of the plants the limestone is insignificant. The sparse fruits and seeds were mostly collected between Linstone and Brambles Chines in the lowest beds of the Upper Headon Series, a laminated grey clay with *Potamomya* having a series of inconspicuous thin discontinuous fine carbonaceous seams. In addition to abundant water plants *Sequoia couttsiae* is common in places and is represented by twigs, seeds and cone scales. Among the rare land plants are seeds of *Zanthoxylum hordwellense, Sambucus* and the ubiquitous older Tertiary *Hordwellia eocenica.* Marsh plants are represented by various Cyperaceae and two Lythraceae. It was at this horizon that the unique fruiting specimen of *Anemia colwellensis* was obtained.

In the overlying pale-buff sands carbonaceous seams are more conspicuous but up to the present the plants found are purely aquatic, e.g. *Brasenia* and *Stratiotes.*

Below the sewer pipe at Linstone Chine there was an incoherent sandy matrix where seeds were more abundant and readily removable by washing and sifting. This was the chief source of the scarce land plants already mentioned. Water plants including *Aldrovanda* were also represented.

In folded beds north of Linstone Chine a dense black patch of seeds yielded only *Brasenia* and *Stratiotes.*

On the whole the flora so far as it is yet known is comparable with that in the more estuarine deposits of the Lower Headon but the scarcity of land plants makes comparison with the Lower Headon of little value.

Almost invariably the plants are preserved as carbonaceous entities which can be isolated from the matrix. Very frequently the cells are replaced in part or even largely by soft amorphous pyrites which is liable to smear when wet and to burst and crack when dry. Consequently the specimens are extremely difficult to preserve permanently and there is a certain amount of distension and distortion. For reasons not understood some genera are more liable to pyritization than others, e.g. *Zanthoxylum* and *Limnocarpus.* The plant list is given on p. 326.

Only about 38 species are known, including *Carpolithus* spp., not all of which are named. Twenty (including *Rhamnospermum*) appear to be marsh or water plants, *Zanthoxylum* and *Sambucus* may have grown on river banks. The conifers, always battered and broken, were probably carried down from the land behind the delta lying at a somewhat higher level together with the chance fragment of *Anemia* and the seeds of *Ficus* and *Rubus.* The Epacridaceae may well have grown on sandy flats or heath land.

The plant assemblage is not a very remarkable or informative one. *Sequoia couttsiae* and *Rhamnospermum bilobatum* are common throughout the Hampshire Basin Tertiary Beds ranging from the London Clay (unpublished record) to the Hamstead Beds and of course occurring in superabundance in the isolated upland Bovey Tracey lake basin. *Caricoidea obscura* and *Hordwellia crassisperma* have been found from the Lower Bagshot upwards. *Ficus lucidus* is also known from the Lower Bagshot and Bournemouth Freshwater Beds. *Myrica boveyana* is present in the Bournemouth Beds, the Highcliff Sands, Lower Headon of Hordle and at Bovey Tracey. *Potamogeton pygmaeus* only becomes common from the Bournemouth Marine Beds upwards to the Upper Headon and *Epacridicarpum headonense* appears first at the same horizon. *Brasenia ovula* and *Limnocarpus forbesi* on the other hand

List of Upper Headon Plants, Colwell Bay, Isle of Wight

Family	Genus and species
Pteridophyta	
Filicales	
Schizaeaceae	*Anemia colwellensis* Chandler
Gymnospermae	
Coniferales	
Araucarineae	? *Araucarites gurnardi* Florin
Taxodineae	*Sequoia couttsiae* Heer
Abietineae	*Pinus* sp.
Angiospermae	
Monocotyledones	
Potamogetonaceae	*Potamogeton pygmaeus* Chandler
	Limnocarpus forbesi (Heer)
Hydrocharitaceae	*Stratiotes headonensis* Chandler
Cyperaceae	*Carex colwellensis* n.sp.
	Carex sp.
	? *Scirpus* sp.
	Caricoidea (? *Cladium*) *colwellensis* n.sp.
	Caricoidea maxima Chandler
	? *Caricoidea angulata* Chandler
	? *Caricoidea obscura* Chandler
	Genus ?
Dicotyledones	
Myricaceae	*Myrica boveyana* (Heer)
	Myrica ? *colwellensis* n.sp.
Moraceae	*Ficus lucidus* Chandler
Centrospermae (Family ?)	Genus ?
Nymphaeaceae	*Brasenia ovula* (Brongniart)
	Genus ? (? *Brasenia ovula*)
	Brasenia spinosa Chandler
	Nymphaea sp.
Droseraceae	*Aldrovanda ovata* (Chandler)
Rosaceae	?*Rubus microspermus* C. & E. M. Reid
Rutaceae	*Zanthoxylum hordwellense* Chandler
Theaceae	*Hordwellia crassisperma* (Chandler)
Lythraceae	*Decodon vectensis* n.sp.
	? *Microdiptera parva* Chandler
Caprifoliaceae	*Sambucus colwellensis* n.sp.
Epacridaceae	*Epacridicarpum headonense* Chandler
	Epacridicarpum colwellense n.sp.
Family ?	*Rhamnospermum bilobatum* Chandler
Incertae Sedis	*Carpolithus colwellensis* n.sp.
	Carpolithus spp.
	Unknown leaf.

while appearing in the Bournemouth Marine Beds range up to the top of the Hamstead Series, although a single doubtful endocarp of the last named has been identified in Cuisian Beds at Whitecliff Bay and its endocarps are known in the Marine Beds of the Selsey peninsula at or about the horizon of the Lutetian-Auversian boundary. The former species again occurs at Bovey. *Microdiptera parva* is a species recorded from the Highcliff Sands, Lower Headon and Bovey, while *Caricoidea maxima* was first described from the Hengistbury Beds. Common to Lower and Upper Headon and scarcely as yet recorded elsewhere are *Stratiotes headonensis* (also in the highest Barton Beds), *Brasenia spinosa, Aldrovanda ovata* and *Zanthoxylum hordwellense. Rubus microspermus* is also a Bovey plant and *Araucarites* and *Anemia colwellensis* probably belong to the species recorded in the Bembridge Beds. Unique, so far, to the Upper Headon are *Carex colwellensis* and other *Carex* species. *Caricoidea* (? *Cladium*) *colwellensis, Myrica* ? *colwellensis* (if indeed it is a *Myrica*), *Decodon vectensis, Sambucus colwellensis. Epacridicarpum colwellense* and *Carpolithus colwellensis.* These species do not appear to have any particular significance; indeed the flora as a whole agrees in a general way with the flora of the Bournemouth Marine and younger Beds, i.e. with that part of the Eocene flora from horizons where conditions of growth may have been affected by the proximity of the sea. The incoming of Hamstead and Bovey species may be noted, for *Rubus* and *Potamogeton* are both represented by other species in older beds.

(b) *The Osborne Beds*

These Beds lie between the Upper Headon Series and the Bembridge Limestone. At Headon Hill Reid & Strahan (1889 : 148) list a grey shale called the " Fish and Plant Beds " but no plants have so far been traced from this locality. Between Headon Hill and Linstone Chine they state (p. 150) the Osborne Series has been removed by denudation and the cliffs consist of the underlying Headon Series. However Osborne Beds reappear beneath the battery at Cliff End at the northern end of Colwell Bay and it is this section which has yielded all but one of the few plant species here described. The section given by Reid & Strahan (1889) mentions leaves in dark shales (" Probably the equivalent of the Fish Bed" noted above).

The remains are poor and fragmentary, *Acrostichum, Nelumbium* and *Dicotylophyllum* having been recognized.

From the Osborne Beds at Osborne a few undersized, immature and somewhat crushed and worn seeds of a *Stratiotes* have recently been obtained and referred provisionally to *Stratiotes neglectus.*

Thus the small plant list of the Osborne Series (see p. 328) contains four species up to date.

Acrostichum ranges from the Lower Bagshot throughout the Eocene where suitable sub-marine conditions prevailed and up into the Bembridge Beds. *Stratiotes neglectus,* if it is this species which is represented, is a typical Bembridge plant but has perhaps been found also in Hamstead Beds. *Nelumbium buchi* occurs at horizons both below wer Headon) and above (Hamstead) and *Dicotylophyllum pinnatifidum* is again a Bembridge species while a fragment has been reported from the Highcliff Sands (Chandler, in press).

List of Osborne Plants, Cliff End, Colwell and Osborne, Isle of Wight

Family	Genus and species
Pteridophyta	
Filicales	
Polypodiaceae	*Acrostichum lanzaeanum* (Visiani)
Angiospermae	
Monocotyledones	
Hydrocharitaceae	? *Stratiotes neglectus* Chandler
Dicotyledones	
Nymphaeaceae	*Nelumbium buchi* Ettingshausen
Incertae Sedis	*Dicotylophyllum pinnatifidum* Reid & Chandler

According to Reid & Strahan (1889 : 157) at this horizon there is " an absence of truly marine beds . . . Purely freshwater strata are also rare. The mass of the clays seems to have been deposited in lagoons, varying in saltness, in which could live brackish-water molluscs like *Melania* and *Potamomya*, and a few of the more hardy freshwater and marine species. Lagoons of this character are at the present day favourite places for turtles and alligators, like those so abundant in this deposit." A reference then follows (p. 158) to the plants discovered by Clement Reid and Henry Keeping at Cliff End although they made no attempt at systematic collecting. The section is now overgrown and not accessible to the public.

(c) *The Bembridge Beds*

The Osborne Beds are succeeded by the Bembridge Beds, a very important member of the Oligocene fluvio-marine series of the Isle of Wight. The lower part of the Bembridge deposits is a massive limestone with shaley bands and some marly beds, the limestone being very definitely a freshwater deposit sharply divided from the mottled Osborne clays below. Although full of *Chara* it has yielded few other recognizable plant remains but Mr. J. F. Jackson obtained from a marly pocket in the limestone of Sticelett Ledge a tiny collection of fruits and seeds all of which occur in the rich Insect Limestone of the overlying Bembridge Marls with its finely preserved flora. Jackson's specimens were listed by Reid & Chandler (1926*a* : 378) and include the following:

Sparganium sp. ?
Stratiotes neglectus Chandler
Cladium sp. [*Caricoidea*]
Brasenia ovula (Brongniart)
Aldrovanda [*intermedia*]
[*Carpolithus* sp. 2]
[*Rhamnospermum bilobatum*]

The information in square brackets was added subsequent to the publication of the note. Only one of the species (*Carpolithus* sp. 2) has been figured and described (see p. 368, Pl. 34, figs. 162–165).

The Bembridge Marls are separated in places from the massive Limestone by some measure of erosion. They demonstrate a change in the conditions of sedimentation, marine shells occurring at the base only. The basal beds are followed by a succession of freshwater and estuarine marls and clays. The bulk of the marls are estuarine in origin as evidenced by the fauna. Wood, fruits and seeds occur at intervals, notably seams comprising masses of *Rhamnospermum bilobatum*, *Stratiotes neglectus* or *Brasenia ovula*, other species being limited in numbers and variety (Reid & Chandler, 1926 : 3). However, the only really rich horizon, so far as present knowledge goes, is the Insect Limestone, a lenticular discontinuous band low in the Marls, a few feet only above the Bembridge Limestone proper. It is described in some detail by Reid & Chandler (1926) and in the various editions of the Geological Survey Memoir. To the information already published about the plants one or two new localities in the Bembridge Marls are now added : Wootton, Ashlake, Werror where *Stratiotes* or *Limnocarpus* or *Brasenia* only have been found (pp. 363–364, 367). There are endocarps of *Celtis* from the Bembridge Limestone of Headon Hill and fine specimens of *Carpolithus* sp. 2 have been collected in the marly pocket in the Bembridge Limestone of Sticelett Ledge mentioned above.

Apart from the above there is little to add to our knowledge of the flora. An unidentified fern (Filix incertae sedis sp. 5 ; Reid & Chandler, 1926 . 39) is now referred provisionally to *Anemia colwellensis* Chandler. *Araucarites gurnardi* Florin is regarded as including the cone scale formerly described as *Doliostrobus* sp. (*Araucarites gurnardi* ?) (Reid & Chandler, 1926 : 52). The pine cone described by Gardner (cf. Reid & Chandler, 1926 : 54) is now regarded as doubtfully belonging to *Pinus dixoni* (Bowerbank) and a *Potamogeton* leaf (Reid & Chandler, 1926 : 67, pl. 3, figs. 23, 24) should no longer be linked tentatively with *P. pygmaeus* as the genus is represented by more than one leaf species including the fine new but unnamed specimen found by the late G. W. Colenutt (Pl. 33, figs. 148, 149). *Epipremnum ornatum* is now referred tentatively only to this genus, a possible alternative alliance being *Raphidophora*, while *Spirematospermum wetzleri* Heer may actually belong to *S. headonense* Chandler. *Celtis edwardsi* is an addition to the flora. The discovery by Colenutt of a finely preserved specimen has enabled the fruits formerly named *Samaravectis ovalis* to be placed in the genus *Ranunculus*. *Carpolithus actinidiformis* is almost certainly a species of *Actinidia* and has been referred tentatively to this genus but given no specific name. Hence there are altogether some 97 species listed including *Dicotylophyllum pinnatifidum* and 13 species of *Carpolithus*. Not all are named, while 15 unnamed species of *Dicotylophyllum* and an unnamed *Phyllites* (which would bring the numbers up to 113) are excluded from the number first mentioned above.

Revised list of Bembridge Plants

Excluding Charophyta. Localities as specified in systematic section.

Family	Genus and species
Pteridophyta	
Filicales	
Polypodiaceae	*Acrostichum lanzaeanum* (*Visiani*)
Schizaeaceae	*Anemia* sp. (? *A. colwellensis* Chandler)
	? *Lygodium* sp.
	Filix Incertae Sedis 5 spp.

Family	Genus and species
Hydropterideae	
Salviniaceae	*Azolla prisca* Reid & Chandler
Equisetales	
Equisetaceae	*Equisetum lombardianum* Saporta
Gymnospermae	
Coniferales	
Araucarineae	*Araucarites gurnardi* Florin
Abietineae	? *Pinus dixoni* (Bowerbank)
	Pinus vectensis Gardner
	Pinus spp. (2 species)
	Pityospermum ambiguum Reid & Chandler
Taxodineae	*Sequoia couttsiae* Heer
Cupressineae	*Cupressus* sp.
	? *Libocedrus* sp.
Angiospermae	
Monocotyledones	
Typhaceae	*Typha latissima* Al. Braun
Sparganiaceae	*Sparganium multiloculare* Reid & Chandler
Potamogetonaceae	*Potamogeton pygmaeus* Chandler
	Potamogeton sp. (formerly *P. pygmaeus* ?)
	? *Potamogeton* spp. (2 species)
	Limnocarpus forbesi (Heer)
	Limnocarpus spinosus Reid & Chandler
Najadaceae	*Naias oligocenica* Reid & Chandler
Hydrocharitaceae	*Ottelia britannica* Reid & Chandler
	Stratiotes neglectus Chandler
Gramineae	Genera (3 species at least)
Cyperaceae	*Carex gurnardi* Reid & Chandler
	Carex sp.
	Cladiocarya foveolata Reid & Chandler
Palmae	*Sabal major* (Unger)
	Palmophyllum sp.
	Palaeothrinax mantelli Reid & Chandler
Araceae	*Epipremnum* ? [or *Raphidophora* ?] *ornata* Reid & Chandler
Zingiberaceae	? *Spirematospermum wetzleri* (Heer) (or *S. headonense* Chandler)
	? *Costus* sp.
	Genus ?
Family ?	*Monocotylophyllum* sp.
Dicotyledones	
Juglandaceae	*Engelhardtia macroptera* (Brongniart)
	Engelhardtia sp.
	Hooleya hermis (Unger)

Family	Genus and species
Betulaceae	*Carpinus* sp.
Fagaceae	? *Fagus* sp.
	? *Quercus* sp.
Ulmaceae	*Celtis edwardsi* n.sp.
Moraceae	*Ficus* sp.
Nymphaeaceae	*Brasenia ovula* (Brongniart)
Ranunculaceae	*Clematis vectensis* Reid & Chandler
	Ranunculus heterostylus Reid & Chandler
	Ranunculus ovaliformis (Reid & Chandler)
Lauraceae	*Cinnamomum lanceolatum* (Unger)
	Neolitsea sp.
Cruciferae	Genus ?
Papaveraceae	*Papaver pictum* Reid & Chandler
Droseraceae	*Aldrovanda intermedia* Reid & Chandler
Rutaceae	*Zanthoxylum* (?) *costatum* Reid & Chandler
Rhamnaceae	*Zizyphus paradisiacus* (Unger) var *paradoxus*
Dilleniaceae	? *Actinidia* sp.
Apocynaceae	*Apocynospermum striatum* Reid & Chandler
	Apocynospermum rostratum Reid & Chandler
	Apocynospermum elegans Reid & Chandler
	Apocynospermum dubium Reid & Chandler
Asclepiadaceae	*Phyllanthera vectensis* Reid & Chandler
	Tylophora antiqua Reid & Chandler
Labiatae	*Melissa parva* Reid & Chandler
	Ajuginucula smithi Reid & Chandler
Bignoniaceae	*Catalpa rugosa* Reid & Chandler
	Radermachera pulchra Reid & Chandler
	Incarvillea pristina Reid & Chandler
Acanthaceae	*Acanthus rugatus* Reid & Chandler
Caprifoliaceae	*Abelia quadrialata* Reid & Chandler
	Abelia quinquealata Reid & Chandler
	Abelia trialata Reid & Chandler
	Abelia sp.4
	Dipelta europaea Reid & Chandler
? Compositae	Genus ?
Family ?	*Rhamnospermum bilobatum* Chandler
	Flabellicula anglica Reid & Chandler
Incertae Sedis	*Carpolithus* spp.2–14
	Dicotylophyllum pinnatifidum Reid & Chandler
	Dicotylophyllum spp.2–16
	Unknown leaf (*Phyllites* sp.)

A reappraisal of this flora is now due having regard to facts and factors previously unknown or only partly recognized. As this is inevitably bound up with general considerations relating to the Eocene floras as a whole, the study of which is now nearing completion, it seems appropriate to defer the matter until the general discussion of these floras takes place in a forthcoming volume where the results of many years of work on fruiting organs in the Tertiary floras of Southern England will be summarized.

(d) *The Hamstead Beds*

The type locality for the Hamstead Beds (spelt Hempstead in older works) is the continuous cliff section at Hamstead and Bouldnor east of Yarmouth which is usually obscured in varying degrees by slipped material. The beds actually occupy a much wider area away from the cliff face, but there are virtually no exposures and in procuring information about the outcrop the Geological Survey officers have had to depend very largely on boreholes. The Hamstead Beds are now usually divided into a lower Freshwater and Estuarine Series with lagoonal deposits which yield a fauna of turtles, crocodiles and freshwater shells together with plant remains, and an upper, much thinner, Marine Series with a few plants in laminated clay near its base. These plants are chiefly the waterlily rhizomes and leaves named *Nelumbium buchi* from the so-called Waterlily Beds and a few palm leaves. In addition, masses of *Brasenia*, *Stratiotes* and *Rhamnospermum* occur at more than one horizon in the Marine Series. There are a few other plants in the lower Estuarine Beds. A well-marked laminated carbonaceous clay called the "Black Band" has been adopted as the base of the Hamstead Beds. The separation here is in fact a matter of convenience for there appears to be no real break between the lower Hamstead Estuarine and the underlying Bembridge Estuarine Beds in spite of some evidence of weathering between the two. Indeed Reid & Strahan state (1889 : 190) " Probably if the beds were now for the first time to be sub-divided, we should class the Bembridge Marls and the greater part of the Hamstead Beds together, and separate the marine beds as the commencement of a new series formed under different conditions." Nevertheless, they continue, " though no palaeontological break occurs at the Black Band, it was so necessary to sub-divide the thick mass of clay above the Bembridge Limestone, that some marked and easily recognisable bed had to be traced. The Black Band proved to be the only horizon that could be followed, and that would give a satisfactory line from which to calculate dips and thicknesses".

Almost all of the few plants so far known are either from the bed called the " White Band " or from the Waterlily Beds. A few species, collected by Colenutt, were in slipped material from an unspecified horizon but undoubtedly above the Black Band. Some specimens in older collections are labelled Lower, or Middle, Freshwater Beds. These names originated with Forbes in the first edition of the Geological Survey Memoir (1856 : 39). Above the Black Band he subdivided the beds into a lower, middle and upper Freshwater Series with " Corbula Beds " above. He adopted the term " White Band " for a " more or less consolidated, often highly ferruginous, band of mingled broken and entire shells, forming a white line in the cliff, and a white streak among the fallen and upturned beds on the shore " (Forbes, 1856 : 43) which he regarded as the junction between his Lower and Middle Freshwater Beds. As, however, the " White Band " has proved to be discontinuous the two horizons cannot really be separated. Moreover, Forbes' Upper Freshwater Beds pass imperceptibly into the *Corbula* Beds and form together with them a single marine division which becomes more truly marine in passing upwards, *Cerithium plicatum* dying out gradually as *Corbula* increases in abundance.

The Geological Survey Museum possesses *Rhamnospermum* and *Stratiotes* collected two feet below the White Band at Hamstead and *Brasenia* from the upper three feet of Forbes' Middle Freshwater Beds. The *Nelumbium* leaves and rhizomes of the Waterlily Bed are part impression and part actual carbonaceous substance now flaking away. *Sequoia couttsiae* may be carbonaceous entities or hollow casts in cementstone. The carbonaceous twigs if preserved in marl can be isolated by washing. This applies to the majority of plant remains which are carbonaceous fruits and seeds, but unfortunately all such are much pyritized and liable to decay. There are few but marsh or water plants known at all and virtually no information is available about the land vegetation of the period, only *Sequoia*, *Sabal*, *Rubus* and ? *Ilex* falling with any certainty into this category. The small plant list is given below. In addition Heer (1862) recorded leaves which he named *Andromeda reticulata* Ettingshausen, describing them as coriaceous and petiolate with reticulate nervation. These have not been included as the determination may need revision.

List of Hamstead Plants

Family	Genus and species
Gymnospermae	
Coniferales	
Taxodineae	*Sequoia couttsiae* Heer
Angiospermae	
Monocotyledones	
Typhaceae	*Typha latissima* Al. Braun
Sparganiaceae	? *Sparganium multiloculare* Reid & Chandler *Sparganium* sp.
Potamogetonaceae	*Potamogeton tenuicarpus* C. & E. M. Reid *Limnocarpus forbesi* (Heer)
Hydrocharitaceae	*Stratiotes neglectus* Chandler *Stratiotes websteri* (Brongniart) *Stratiotes acuticostatus* Chandler
Cyperaceae	? *Caricoidea minima* (Chandler)
Palmae	*Sabal major* (Unger)
Dicotyledones	
Nymphaeaceae	*Brasenia ovula* (Brongniart) *Nelumbium buchi* Ettingshausen
Rosaceae	*Rubus* sp.
Leguminosae	Genus ?
Droseraceae	*Aldrovanda intermedia* Reid & Chandler
Aquifoliaceae	? *Ilex* sp.
Family ?	*Rhamnospermum bilobatum* Chandler
Incertae Sedis	*Carpolithus* sp. (? *Spirematospermum* sp.) *Carpolithus* spp.

Among the Hamstead plants *Sequoia couttsiae* links the Beds with all earlier Tertiary horizons and with the Bovey Tracey lake basin further west. Its broken and battered remains suggest that it may have travelled a considerable distance. Species of *Sabal* and *Rhamnospermum bilobatum* also occur in older Tertiary beds and *Limnocarpus forbesi* in all down to at least the Bournemouth Marine stage. The water plants *Potamogeton tenuicarpus, Stratiotes websteri* and *Brasenia ovula* are also found at Bovey Tracey. *Typha latissima, Sparganium multiloculare, Stratiotes neglectus, Aldrovanda intermedia* occur in the underlying Bembridge Beds, *Caricoidea minima, Nelumbium buchi* in the Lower Headon of Hordle, the latter also in the Osborne Beds. *Stratiotes acuticostatus* has not yet been recorded at any other horizon.

It is clear that up to date there are virtually no characteristics known by which the flora of the Hamstead Beds can be unmistakably distinguished but the most significant species appear to be *Stratiotes websteri, S. acuticostatus* and *Potamogeton tenuicarpus* which here appear for the first time.

(e) *Horizon* ? Locality Headon Hill (in ironstone).

Icacinaceae *Stizocarya* sp.

As always my debt to others is great and I acknowledge, although inadequately, much help received from my friends and colleagues Dr. K. I. M. Chesters and Mr. F. M. Wonnacott in the preparation of this manuscript.

SYSTEMATIC DESCRIPTIONS

(a) *The Upper Headon Beds*

All material from Colwell Bay, Isle of Wight.

PTERIDOPHYTA
Order FILICALES
Family SCHIZAEACEAE
Genus ***ANEMIA*** Swartz
Anemia colwellensis Chandler

1955 *Anemia colwellensis* Chandler, p. 304, pl. 35, figs. 39, 40, 42–53; pl. 36, figs. 59–64; text-fig. 2, 1.

The species was fully described and illustrated in the above work. The solitary pinnule fragment yielded sporangia and spores. Slides V.31519–23 were figured in 1955. There are a few unfigured slides: V.42034–35 show fragments of sporangia, V.42036 shows also fragments of annulus and paraphyses. V.42037 paraphyses, V.42033 annulus and spores. The pinnule fragment came from the lowest Upper Headon Beds between Brambles and Linstone Chines.

GYMNOSPERMAE

Order CONIFERALES

Family ARAUCARINEAE

Genus ***ARAUCARITES*** Presl, 1838 : 203

? Araucarites gurnardi Florin

(Pl. 27, figs. 1, 2 ; Text-fig. 1)

1926 *Doliostrobus* sp. (*Araucarites gurnardi* ?) Reid & Chandler, p. 52, pl. 2, figs. 17, 18.

Description. The upper (distal) part of a broadly oval cone-scale closely comparable in form with scales from the Bembridge Beds but somewhat smaller. Length of scale incomplete ; maximum breadth (almost perfect), 6 mm. ; maximum thickness, 1·25 mm. (Length and breadth of Bembridge scales, 11 mm.) Form of base not seen ; apex with short conical mucro (? shortened by abrasion). Dorsal surface with conspicuous transverse projection about 2 mm. below the tip of the mucro, producing a facet between mucro and ridge which no doubt formed the " escutcheon " at the surface of the cone (Pl. 27, fig. 1). Ventral surface with only a slight transverse ridge about 1·25 mm. below the tip of the mucro (Pl. 27, fig. 2). Beyond the ridges the distal end of the scale is smooth on both sides. Below the ridges the surfaces are longitudinally striate. There is a smooth marginal rim at the distal end on each side of the mucro along which the cells are aligned parallel with the margin, but elsewhere in this region of the scale there appear to be longitudinally elongate cells on the dorsal surface producing longitudinal striations, but the structure is much obscured by sand-pitting. Similar longitudinal striations are particularly conspicuous on the dorsal surface over the limb of the scale below the projecting ridge. On the ventral surface the cells are transversely aligned over the ridge, but immediately below it they are equiaxial, rounded and coarse (bordered pits ?), about 0·016 to 0·025 mm. in maximum diameter. Beyond, on the limb below the ridge on this surface they are rectangular oblong, narrow and small, often sunken but with raised walls.

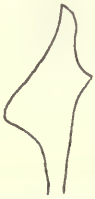

Fig. 1. ? *Araucarites gurnardi* Florin. Diagrammatic longitudinal section of a scale perpendicular to the ovuliferous surface.

Remarks. The scale (V.43780) shows the characters of Araucarineae and agrees with *Araucarites*. It so closely resembles scales from the Bembridge Beds (Reid & Chandler, 1926 : 52, pl. 2, figs. 17, 18) named *Doliostrobus* sp. (*Araucarites gurnardi* ?) that in spite of its somewhat smaller size there can be little doubt that they belong to a single species. Comparable differences in size occur among scales of living *Agathis* and *Araucaria* and in the fossil form, *Doliostrobus sternbergi* Marion (1888), the size depending on the position in the cone. The Bembridge scales were not referred definitely to *Araucarites gurnardi* (Reid & Chandler, 1926 : 48, pl. 2, figs. 6–19) because they were not in organic continuity with the foliage so named present on the same blocks of matrix. On the grounds of generic similarity reference was made to Marion's genus *Doliostrobus* from Alais where cones and cone-scales were in organic continuity with foliage of *Araucarites* type. In the light of further experience notably with associated foliage and a cone-scale at Selsey (Chandler, 1961*a* : 23, pl. 4, figs. 1–5 ; pls. 5, 6) it now appears reasonable to name the Bembridge scales *Araucarites* definitely and regard them as belonging to the foliage *A. gurnardi*, the similar scale from Colwell being placed in this species also. The cone-scales of *A. gurnardi* differ both from *A. selseyensis* and *Doliostrobus sternbergi* in their less attenuated base, less elongate form and in the shorter less parallel-sided mucro although it is possible that the mucro of *A. gurnardi* may have suffered some reduction by abrasion. Further the angle of inclination of the distal margins of the scale is not so sharp as in *A. selseyensis* or *Doliostrobus*. There now appears to be little or no doubt that *Doliostrobus sternbergi* should also be regarded as an *Araucarites*.

Family TAXODINEAE

Genus ***SEQUOIA*** Endlicher

Sequoia couttsiae Heer

(Pl. 27, figs. 3, 4)

1962 *Sequoia couttsiae* Heer : Chandler, p. 20, pl. 4, figs. 1–32; text figs. 1–6. See also for earlier references.

Typical small twig tips which occasionally yield fragments of cuticle occur with a fair degree of frequency. They and their cuticles, also cone-scales and seeds were described and figured among material from other horizons by Chandler (1962 : 20, pls. 1–3 ; pl.4 , figs. 1–32 ; text-figs. 1–6). A few twigs bear small tufts at their extremities which appear to be male cones (V.43781–82). They are embraced by two falcate leaves the whole giving a subtriangular outline (Pl. 27, fig. 3). Within these basal leaves are branched structures with feathery extremities (slide V.44841). On maceration in nitric acid they become somewhat translucent and are seen to bear elliptical anthers with large gaping mouths (Pl. 27, fig. 4) from which pollen could be obtained. The seeds are much pyritized, frequently with a curved seed-body. Some have split marginally, as for germination, into two equal valves. The wings are commonly battered and frayed and the surface is usually rather poorly preserved. Many specimens were collected between Brambles and Linstone Chines (V.43783–84). The male cones were found between Colwell and Brambles Chines.

Family ABIETINEAE

Genus ***PINUS*** Linnaeus

Pinus sp.

(Pl. 27, fig. 5)

DESCRIPTION. *Seed :* Sub-obovoid, somewhat compressed and bisymmetric, apparently dehiscing for germination into two valves. One margin of the seed is convex, the other has a sigmoidal curvature near the narrow end which gives rise to a slightly curved beak. Micropyle at tip of beak. One surface of seed perfect, flat, with narrow elongate cells arranged in parallel groups. The cell groups are variously oriented producing a complicated pattern, as in many species of *Pinus*, on the side of the seed covered by the wing, i.e. the uppermost side as it lay on the cone-scale. These cells are about 0·7 mm. long, 0·007 to 0·009 mm. broad, they show single lines of pits about 0·006 to 0·008mm. in diameter which give a finely toothed effect where they abut against the cell walls. The ends of the cells are often rectangular. Opposite lower surface of seed convex, now incomplete, this valve has been broken longitudinally in fossilization so that two-thirds of its breadth are missing and one-third adheres to the other valve along the natural suture plane. The suture plane of the opposite margin has been exposed where the valve separated and shows cells aligned parallel with its outer edge. The broken edge of the imperfect valve is formed of broad cells about 0·076 by about 0·038 mm. aligned at right angles to the surface (seen at *c* in Pl. 27, fig. 5). Length of seed, 4·5 mm. ; breadth, 2·2 mm. ; thickness (not quite complete), 0·75 mm. Wing only preserved as a few decayed patches of tissue on the flat upper surface of the seed.

REMARKS. The form and cell structure indicate the genus *Pinus*. The living *P. breweriana* resembles it in form and size but the cell structure of the upper surface is simpler. Many species of *Pinus* show the complex arrangement of wing cells seen in the fossil. Seed (V.43785), preserved in soft pyrites mud, from between Brambles and Linstone Chines.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus ***POTAMOGETON*** Linnaeus

Potamogeton pygmaeus Chandler

(Pl. 27, figs. 6–8)

1961*b* *Potamogeton pygmaeus* Chandler : Chandler, p. 103, pl. 24, figs. 3–6. See also for earlier references.

The species has been fully described from the Lower Headon of Hordle, Hants., and the Bembridge Beds, Isle of Wight. It is also now recorded from the Bournemouth Marine Beds and Bournemouth Freshwater Beds (one only) (Chandler, in press).

The Upper Headon of Colwell has yielded the most beautifully preserved carbonaceous endocarps yet seen, many showing the spine bases so often abraded in other material. The style, terminal on the ventral margin, is shown in Pl. 27, figs. 6, 7 and the median ventral spine in Pl. 27, fig. 6. Spine bases on keel can be seen in Pl. 27, figs. 6, 7 the long slender tips being broken. Perfect spines have only been found as impressions in the Bembridge Insect Limestone (Reid & Chandler, 1926, pl. 3, fig. 21).

The hyaline testa of the curved seed remains within the Colwell endocarps. The endocarps show externally the typical regular quadrilateral cells aligned parallel with the curvature. The great variation in size is noticeable and the slender form with large gap between the limbs is clearly visible in abraded material as the exocarp is almost invariably missing. The germination valve, crested medianly longitudinally, normally carries its spine bases but in some crushed specimens (Pl. 27, fig. 8) these are inconspicuous. These particular specimens are of unusual appearance as they are internal casts with only adherent remains of endocarp somewhat obscured by sand. Owing to compression the thickened limbs appear to lie closer together than in more normally preserved endocarps the gap between them being partly obliterated. These specimens lay on a flat bedding plane in beds with *Potamomya* and were associated with casts of Ostracods. The endocarp figured in Pl. 27, fig. 8 has been removed from its matrix. It and V.43789–91 are from beds between Brambles and Linstone Chines, V.43792 in folded beds near Fort Victoria boundary fence. The other figured specimens were below the sewer trench at Linstone Chine.

Genus ***LIMNOCARPUS*** Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus forbesi (Heer)

(Pl. 27, figs. 9, 10)

1961*a* *Limnocarpus forbesi* (Heer) : Chandler, p. 28, pl. 7, figs. 22–24. See also for earlier references.

1961*b* *Limnocarpus forbesi* (Heer) : Chandler, p. 104, pl. 24, figs. 7–11.

Endocarps of this species are among the common plants of the Upper Headon Beds. The specimens are exactly comparable in character with those from the Lower Headon at Hordle and there is nothing to add to previously published descriptions of the species. However, unlike the Hordle specimens, the Colwell endocarps are commonly pyritized in the same manner as are the Zanthoxyleae (p. 349). The soft amorphous pyrites has replaced the carbonaceous tissues, reproducing their form exactly, but it readily smears and on drying expands and cracks with resulting disintegration of the specimens. As at Hordle these water plants must have formed dense masses probably of floating weed growing in lagoons and stagnant channels of water. In addition to the figured specimens there are V.43796–97 from beds between Brambles and Linstone Chines and V.43798 from folded beds near the Fort Victoria boundary fence. Also 52898 Toulmin Smith Coll. 1877 " shale bed with seeds " which may be Upper or Lower Headon.

Szafer (1961 : 172, pl. 22, figs. 16–21) has recently described a *Ruppia* (*R. maritima* L. var. *miocaenica*) with a strongly papillate or rugose surface from the Miocene flora of Stare Gliwice, Poland. It bears some resemblance to *Limnocarpus forbesi* but is clearly a *Ruppia* rather than a *Limnocarpus*. He regards it as differing only from the living *Ruppia maritima* in its more papillate fruits. In the same work (1961 : 174, pl. 22, figs. 23–26) he also described a larger slightly papillate species *Ruppia major*. He considers it to be related to *Limnocarpus*. If so it is more closely akin to *L.* ? *enormis* (Chandler, 1961*a* : 29, pl. 7, figs. 25–33) than to *L. forbesi*, but *L.* ? *enormis* is even larger and belongs to *Limnocarpus* rather than to *Ruppia*.

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes headonensis Chandler

(Pl. 27, figs. 11–19)

1961*b* *Stratiotes headonensis* Chandler: Chandler, p. 104, pl. 24, fig. 17. See also for earlier references.

The species has been so fully described in 1923 and 1961*b* that it is unnecessary to repeat the information which is equally applicable to the new material from the Upper Headon of Colwell. Thus *Stratiotes headonensis* now ranges from the top of the Barton Beds to the Upper Headon. Typical Upper Headon specimens are illustrated (Pl. 27, figs. 11–14) while seeds from the Lower Headon of Hordle are figured for comparison (Pl. 27, figs. 16–19). In addition to figured Colwell material there are V.43804 from beds between Brambles and Linstone Chines; V.43805 in sand and clay south of Linstone Chine above the Oyster Bed; V.43806 from folded beds close to Fort Victoria boundary fence. One box of seeds labelled " Bembridge Series " certainly belongs to *S. headonensis* but is probably from Colwell.

Family CYPERACEAE

Genus ***CAREX*** (Dill.) L.

Carex colwellensis n.sp.

(Pl. 28, figs. 26, 27)

DIAGNOSIS. Endocarp triangular with obovate facets, of which the greatest breadth lay at about the middle. Surface cells with raised walls and central papillae. Length of cells variable, some equiaxial, breadth from 0·01 to 0·016 mm. Length of endocarp, 1·5 mm.; breadth, 0·75 by 0·5 mm.

HOLOTYPE. V.43808.

DESCRIPTION. *Endocarp:* Three-angled, three-sided, each facet being obovate. One facet somewhat narrower than the other two. Greatest breadth at about the middle. Style patent very shortly trifid (worn). Splitting tends to occur along the angles starting at the base. Surface formed of somewhat elongate cells with slightly raised walls some of which show remains of a raised central papilla. Margins of cells very finely toothed. Length of cells variable some being equiaxial, breadth about 0·016 mm. at the middle of the endocarp, 0·01 mm. near the apex. Length of endocarp 1·5 mm. including style base; breadth, 0·75 by 0·5 mm.

REMARKS. A typical triangular *Carex*. The most comparable living species seen were *Carex flava* and *C. oederi*, both of which have smaller and more rounded surface cells. The solitary specimen is so beautifully preserved as to be " recent " in appearance but its pyritized condition established it as a genuine fossil. Round black patches on the surface suggest pustules due to fungus. From beds between Brambles and Linstone Chines.

Carex sp.

(Pl. 28, figs. 20–25)

Description. *Endocarp :* Obovate in outline with one surface flat and the other slightly inflated at the middle with an obscure median longitudinal angle flanked by two facets. All now much compressed so as to be nearly flat. The greatest breadth is at about three-quarters of the length from the base. Apex rounded, style obscure (? due to abrasion). Surface formed of polygonal or hexagonal, somewhat elongate, longitudinally aligned cells about 0·016 to 0·025 mm. broad. The cells have slightly raised walls. One perfect endocarp was 1·3 mm. long, 0·8 mm. broad. Another endocarp (slightly imperfect at the base) was 1·3 mm. long, 0·75 mm. broad. Only one (V.43807) is still extant owing to their poor condition on discovery. All from beds between Brambles and Linstone Chines.

Genus ***SCIRPUS*** (Tourn.) L.

? Scirpus sp.

(Pl. 28, fig. 28)

Description. *Endocarp :* Obovate, somewhat truncate at the base where there is a large aperture. Apex with stout stylar mucro about 0·2 mm. long. Surface ornamented with about six rounded longitudinal ribs separated by deep sharp furrows. Coat forming ribs spongy, close-textured, of very minute cells having a tendency to produce transverse striations. Basal aperture closed by a small circular plug convex externally at its centre from which small cells radiate. Length of endocarp, 2 mm. ; breadth, 1 mm.

Remarks. The near relationship of this unique specimen (V.43809) has not been conclusively established but it probably belongs to the group Caricoideae, or to Scirpoideae and perhaps to *Scirpus* as suggested by the basal aperture with plug and the apical mucro. It is quite distinct in the form of its rounded longitudinal ribs from *Scirpus lakensis* (Chandler, 1962 : 50, pl. 6, figs. 7–18) from the Lower Bagshot and Bournemouth Freshwater Beds and from Cuisian Beds in the Selsey Peninsula (Chandler, 1961*a* : 18, 33).

Genus ***CARICOIDEA*** Chandler, 1957 : 86

Caricoidea (?Cladium) colwellensis n.sp.

(Pl. 28, figs. 31–35)

Diagnosis. More or less bisymmetric oburceolate endocarp resembling *Cladium* in form but having a plate-like expansion at the base of the neck, sometimes split radially in line with two longitudinal ridges in the plane of symmetry. Surface with irregular low rugosities. Length of endocarp, 1·5 to 2·25 mm. ; breadth, 1 to 1·75 mm.

Holotype. V.43810.

Description. *Endocarp :* Oburceolate with marked apical mucro, conspicuous contracted neck spreading out below to form a circular plate-like base often broader than the endocarp itself. Approximately bisymmetric with rounded longitudinal ridges extending from the mucro in the plane of symmetry on each side to the edge of the neck. Plate-like base sometimes indented or split radially along the line of these ridges forming in such specimens a pair of basal flanges rather than a plate (Pl. 28, figs. 32, 34). Surface of endocarp covered with irregular low rugosities. Basal aperture small (Pl. 28, fig. 35). Rugose outer coat, about 0·15 to 0·2 mm. thick, formed of spongy hollow cells about 0·025 mm. in diameter. In section a thin coarsely columnar inner coat is seen about 0·025 mm. thick. Cavity lined by transversely oriented cells (testa of seed ?) which are finely toothed, the narrower diameter from top to bottom being about 0·016 mm. There is also a longitudinally striate layer with cell walls (striae) about 0·016 mm. apart. Dimensions of endocarps : 1)Length, 1·7 mm. ; breadth, 1·5 mm. ; breadth of neck, 1·2 mm. 2) Length, 1·75 mm. ; breadth, 1 mm. ; breadth of neck, 1·2 mm. 3) Length, 1·5 mm. ; breadth, 1·15 mm. ; breadth of neck, 1·5 mm. 4) Length, 1·5 mm. ; breadth, 1 mm. ; breadth of neck, 1·1 mm. 5) Length, 1·75 mm. ; breadth, 1·25 mm. 6) One exceptionally large endocarp length, 2·25 mm. ; breadth, 1·75 mm. ; breadth of neck, 1·75 mm.

Remarks. The fruit (utricle) has not been seen. The endocarps obviously belong to Caricoideae and are closely related to and probably identical with *Cladium*. They differ from living representatives of this genus so far seen and from comparable fossil species in the irregular rugosities of the external surface and in the plate-like basal expansion of the neck. One specimen (now decayed) showed the basal expansion seated on a pillow-like receptacle. An expansion was present in a lesser degree in specimens from the Pliocene of Bidart (C. & E. M. Reid, 1915 : 424, pl. 7, fig. 30) and is developed in a peculiar way as a wide pierced plate with large foramina in *Cladium reidiorum* Nikitin (*in* Dorofeev, 1958 : 172, pl. 1, fig. 33 from the Oligocene of Western Siberia ; 1959 : 168, pl. 3, figs. 9–11, from the Miocene of the Rostov Region) and in a slightly lesser degree in *Cladium macrocarpum* Dorofeev and *C. europaeum* Dorofeev from the Tertiary of Byelorussia (Dorofeev, 1960 : 1428, pl. 3, figs. 7–12). The apical mucro is very well developed also the longitudinal ribs. While therefore they may belong to *Cladium* it seems better until information about the fruit is forthcoming to refer them only provisionally to *Cladium* leaving them for the present in the form-genus *Caricoidea.*

Szafer (1961 : 90, pl. 24, figs. 17–23) refers endocarps of this type without hesitation to *Cladium mariscus* R.Br., *foss.* They came from the Miocene of Stare Gliwice, Poland.

In addition to the figured material there are V.43813–14. All were found between Brambles and Linstone Chines. One endocarp (decayed) was from the folded beds near the Fort Victoria boundary fence.

Caricoidea maxima Chandler

(Pl. 28, figs. 36–40)

1960 *Caricoidea maxima* Chandler, p. 207, pl. 31, fig. 35.

Emended Diagnosis. Fruit obovoid or truncate subovoid with deep depression in the truncate base. Length of fruit, 3·2to 4·25 mm. ; greatest breadth, 2·25 to 3·25 mm. Endocarp subglobular or shortly oburceolate, with or without apical mucro, with short basal neck and two opposite longitudinal ridges. Length of endocarp, 1·5 to 2 mm.; breadth, 1·4 to 2 mm.

SYNTYPE. V.43815.

DESCRIPTION. *Fruit:* Obovoid to truncate subovoid frequently somewhat flattened laterally, with basal truncation which is pierced by a large subcircular or circular opening. Obtusely pointed at the apex. Surface always abraded as no specimen has been seen showing the outer shining epidermal layer. Wall woody, up to at least 0·6 or 0·7 mm. thick, close-textured, formed of equiaxial cells about 0·022 mm. in diameter. Length of fruit, 3·2 to 4·25 mm.; greatest breadth, 2·25 to 3·25 mm.

Endocarp: Usually situated nearer to the apex than the base within the thick woody fruit. Shortly oburceolate or subglobular sometimes with small apical mucro. Basal aperture with neck which may be very short and is closed by a plug. Aperture opening into a short canal in the fruit wall leading to its basal opening. Surface close-textured, finely pitted, pits 0·012 to 0·016 mm. in diameter, with two longitudinal opposite external ridges. Formed, as seen in section, of a thin outer layer with obscure structure and an inner columnar coat which is about 0·23 mm. thick. Lining layers much decayed but showing traces of horizontally aligned digitate cells. Length of endocarp, 1·5 to 2·2 mm.; breadth, 1·4 to 2 mm.

REMARKS. One fruit and two detached endocarps, all figured. Two other figured specimens have now decayed. The species was based on a fruit from the Hengistbury Beds (reference given above), but information about the endocarp is now available for the first time. The diagnosis is therefore expanded. *Caricoidea maxima* resembles *C. minima* from the Lower Headon of Hordle, but the fruit is considerably larger and the endocarp is larger and more subglobular. It may also be present at Hordle as a similar specimen was seen there, but unfortunately it decayed before it could be described.

? ***Caricoidea angulata*** Chandler

(Pl. 28, figs. 41, 42)

Caricoidea angulata Chandler (in press), p. 66, pl. 9, figs. 1–23; text-fig. 12.

DESCRIPTION. *Fruit:* Not seen.

Endocarp: Detached from fruits. Body of endocarp narrowing gradually or more suddenly to form a basal neck, apex narrowed to a mucro, well marked in some better preserved specimens (Pl. 28, fig. 41) abraded in others (Pl. 28, fig. 42). Surface abrasion makes it difficult to see the regular even pitting characteristic of *Cariocoidea angulata*. Dimensions of endocarps: 1) Length, 1·5 mm.; breadth, 1·25 mm. 2) Length, 1·7 mm.; breadth, 1·3 mm. 3) Length, 1·75 mm.; breadth, 1·3 mm.

REMARKS. In addition to two figured specimens, there are V.43820–23 all from between Brambles and Linstone Chines. In the absence of evidence about the fruit and in view of the abraded condition the determination of the species is provisional, but the size agrees with that of *C. angulata* and the endocarps are smaller than those of *C. maxima* and larger than those of *C. obscura*.

? *Caricoidea obscura* Chandler

(Pl. 28, figs. 29, 30)

1960 *Caricoidea obscura* Chandler, pp. 207, 223, pl. 30, figs. 27–33 ; pl. 33, figs. 98–105.
1961*a* *Caricoidea obscura* Chandler : Chandler, p. 33, pl. 7, fig. 34.
1961*b* *Caricoidea obscura* Chandler : Chandler, p. 106, pl. 24, figs. 22–24.
1962 *Caricoidea obscura* Chandler : Chandler, p. 52, pl. 6, figs 20–33 ; text-fig. 9.
Caricoidea obscura Chandler : Chandler (in press), p. 65, pl. 8, figs. 42–56.

DESCRIPTION. *Endocarp :* Oburceolate narrowing gradually to a mucronate apex and contracting suddenly to a narrow basal neck. Some specimens show a pair of longitudinal ribs. Outer surface smooth (although sometimes rough secondarily through decay in fossilization) showing traces of very fine cells and pitting. Wall in section about 0·1 mm. Locule lining obscure. Dimensions of endocarps : 1) Length, 1·25 mm. ; breadth, 1·05 mm. 2) Length, 0·9 mm. ; breadth, 0·8 mm. 3) Length, 1 mm. ; breadth, 0·9 mm. 4) Length, 1 mm. ; breadth, 0·8 mm. 5) Length, 0·9 mm. ; breadth, 0·75 mm.

REMARKS. The small size of these isolated endocarps suggests *Caricoidea obscura* but as the fruits have not been seen the determination is provisional. Endocarps from the Lower Headon of Hordle are equally small. Those from the Lower Bagshot are slightly larger. The Highcliff Sands specimens are closely comparable in size although some are relatively broader. In addition to two figured endocarps there are V.43825 and V.43827, all from between Brambles and Linstone Chines and V.43828 an endocarp in folded beds close to Fort Victoria boundary fence.

Family CYPERACEAE

Genus ?

(Pl. 28, figs. 43, 44)

DESCRIPTION. *Fruit :* Rounded elongate triangular in outline, apex broken, sides tapering gradually to the base which is somewhat blunt. Probably originally more or less pointed at the apex. The fruit may have been triangular in transverse section with one broad facet occupying the whole breadth and two narrow ones meeting in a longitudinal angle having a groove along its crest. External surface longitudinally striate, between the striae are lines of equiaxial cells about 0·01 mm. in diameter. Internal surface where exposed by splitting on drying showing conspicuous transverse alignment of cells. Length of fruit, 2·2 mm. ; breadth, 1·1 mm. No endocarp has been seen.

REMARKS. Cell structure and form suggest Cyperaceae and possibly *Carex* but in view of the poor condition and the fact that there is only one specimen (V.43829) it appears inadvisable to make more than a tentative reference to the family.

V.43830 is a small triangular endocarp belonging to the family Cyperaceae but it is unlike other species described.

Class DICOTYLEDONES

Family MYRICACEAE

Genus ***MYRICA*** Linnaeus

Myrica boveyana (Heer) pars

(Pl. 29, figs. 45–48)

1862*a* *Carpolithus boveyanus* Heer, p. 1077, pl. 70, figs. 7–14 (in part).
1957 *Myrica boveyana* (Heer) pars Chandler, p. 90, pl. 12, figs. 45–48.
1961*b* *Myrica boveyana* (Heer) pars: Chandler, p. 110, pl. 25, figs. 33, 34.

DESCRIPTION. *Endocarp:* Bisymmetric, germinating by splitting into equal valves in the plane of symmetry, oval in outline, somewhat compressed at right angles to the plane of symmetry. Outer surface with obscure rugosities over the central area, very slightly flattened around the margin. A few superficial fibres have a general longitudinal arrangement, some appear to enter the thickness of the endocarp near a small basal scar. Locule, as revealed on inner surface of valve after germination, urceolate in outline tapering into an apical stylar canal; suture about 0·6 mm. broad, flat. Base with short funicular canal still carrying a fibre. Cells of locule lining diverge from style and funicle; locule longitudinally striate, the striae due to elongate polygonal cells which appear to have finely toothed walls, largest at the middle of the endocarp where they may be 0·05 mm. long and 0·027 mm. broad. Length of endocarp, 3·75 mm.; breadth, 3·1 mm.; thickness, 2·25 mm. Second specimen (represented by one, slightly imperfect, much abraded valve): length, 3·25 mm.; breadth, 2·75 mm.; thickness (estimated), 2 mm. Small endocarp: length, 2·5 mm.; breadth, 1·75 mm. (V.43833).

REMARKS. The endocarps are comparable with those from Bovey Tracey but are larger than the Hordle specimens. From between Brambles and Linstone Chines.

Myrica? colwellensis n.sp.

(Pl. 29, figs. 49–55)

DIAGNOSIS. Endocarp subovoid with about six regular low rounded external longitudinal ribs on each valve separated by sharp furrows which carry fibres. Length of endocarp about 2·8 to 3 mm.; breadth about 2 to 2·5 mm.

HOLOTYPE. V.43834.

DESCRIPTION. *Endocarp:* Bisymmetric, germinating by splitting into two valves in plane of symmetry. Subovoid but somewhat compressed at right angles to the plane of symmetry, having a slight basal mucro and evenly rounded apex. External surface with about six regular low rounded ribs on each valve with a longitudinal fibre in each of the sharp furrows between them. The fibres extend almost from the basal attachment scar to the apical style. Locule compressed urceolate, narrowed to the stylar canal, having a short funicular canal at the base. Suture plane 0·4 to 0·5 mm. broad near the base. Locule lining of finely toothed more or less equiaxial cells about 0·05 mm. in diameter. Texture of wall compact. Length of endocarp, 2·8 mm.; breadth, 2 mm.

REMARKS. The holotype is represented by its two separated valves one slightly imperfect. There is also a single abraded valve of another slightly larger specimen (V.43836) and the basal end of one valve of a third broader endocarp (V.43835), V.43837 is a broken and unfigured valve. The reference of this species to *Myrica* must be regarded as doubtful, but on the whole the resemblance is greater than to *Carpinus* which has a similar compressed urceolate locule. *Carpinus* may show uneven fluting of the surface as in *C. betulus* but not regularly longitudinal lobing, while the well marked fibres always overlie longitudinal ridges not the intervening furrows as in the fossil. The form of the endocarp in *Carpinus* is pointed ovate not a regular oval in outline. All specimens are shrunken and diminished in size through drying. Position of placenta not clear.

Family MORACEAE

Genus ***FICUS*** Tourn.

Ficus lucidus Chandler

(Pl. 29, fig. 56)

1962 *Ficus lucidus* Chandler, p. 58, pl. 7, figs. 13–18 ; text-fig. 11.
Ficus lucidus Chandler : Chandler (in press), p. 76, pl. 11, figs. 13–15.

DESCRIPTION. *Carpel :* Subovoid originally, now crushed, both diameters being increased thereby. The carpel has burst and split marginally at the stylar end. Surface formed of minute equiaxial cells. Length, 1·5 mm. ; breadth, 1·25 mm. as crushed.

REMARKS. The single specimen (V.43838) from beds between Brambles and Linstone Chines is identical in general morphological characters and cell structure with better preserved material from the Dorset Pipe-clay Series and the Bournemouth Beds (references above).

Order CENTROSPERMAE

Family ?

Genus ?

(Pl. 29, fig. 57)

DESCRIPTION. *Seed :* Small curved, transversely oval in outline, with asymmetrically placed marginal hilum between the unequal limbs marked by a small projection. Surface smooth apparently formed of somewhat obscure digitate cells with few digitations, the cells about 0·027 mm. in diameter. Dimensions of seed, 0·9 by 0·75 mm.

REMARKS. The form and digitate cells suggest Centrospermae, possibly even Caryophyllaceae, but the material is too poor and limited for further determination. The seed has begun to split starting at the hilum and in a direction between the limbs. The solitary specimen, V.43839 came from beds between Brambles and Linstone Chines.

Family NYMPHAEACEAE

Genus ***BRASENIA*** Schreber

Brasenia ovula (Brongniart)

(Pl. 29, figs. 58, 59)

1926 *Brasenia ovula* (Brongniart) Reid & Chandler, p. 99, pl. 6, figs. 15–18. See also for earlier references.
1957 *Brasenia ovula* (Brongniart) : Chandler, p. 96, pl. 13, fig. 75.
1961*b* *Brasenia ovula* (Brongniart) : Chandler, p. 116.

The species is one of the commonest plants in the Lower Headon of Hordle and the Isle of Wight and successive beds of the Oligocene in the Isle of Wight and at Bovey Tracey. It usually occurs in seams blackened by its seeds and some of the seed-beds mentioned by Reid & Strahan (1889) are made up almost exclusively of these seeds. As in all localities where *Brasenia ovula* occurs there is very great variation in shape and size. The species is too well known for further description to be necessary as all previous accounts are equally applicable to the Upper Headon material. In addition to figured material which comes from beds south of Brambles Chine, there are seeds from between Brambles and Linstone Chines (V.43842) and from folded beds close to Fort Victoria boundary fence (V.43843).

Genus ? ***(?Brasenia ovula)***

(Pl. 29, fig. 62)

DESCRIPTION. *Seed :* Crushed dorsiventrally so that the original form is obscured but the slightly conical embryotega is clearly seen with its central micropylar aperture. The embryotega is about 0·6 mm. in diameter. Its limits as it lies in the testa are rather obscure since it has not begun to separate from the surrounding tissues. Its cells are radially aligned around the central aperture, largest at the circumference where they are about 0·05 mm. in diameter, convex with rounded outlines having a slight tendency only to be sinuous. Surface of seed itself formed of digitate cells like those of *Brasenia ovula* with few (about five or six) digitations which are short and rounded. Each cell is somewhat convex superficially and the alignment is in longitudinal rows diverging from the embryotega. The cells show signs of separating from each other perhaps as a result of crushing. They are coarser than those of typical *B. ovula* and more inflated, the larger ones about 0·1 mm. in diameter. Tegmen translucent. Diameter of crushed seed, 3 by 2·6 mm.

REMARKS. The large seed falls within the range of size of *Brasenia ovula*. Its peculiar apperance may be the result of crushing, but it has been related to this species only provisionally. V.43852 from between Brambles and Linstone Chines.

Brasenia spinosa Chandler

(Pl. 30, figs. 63–69)

1961*b* *Brasenia spinosa* Chandler : Chandler, p. 117. See also for earlier references.

DESCRIPTION. *Seed :* Subglobular to ovoid, anatropous with circular aperture at one end, often gaping but sometimes closed by an embryotega. External surface with rounded longitudinal ridges sometimes corresponding with lines of cells and with rows of sporadic tubercles which may be blunt, short and rounded or longer and spiney. They are frequently broken. Tubercles may arise from the centre of a digitate cell 0·05 to 0·1 mm. in diameter although not every cell bears a tubercle. Sometimes the tubercles or rugosities are not related to the cell outlines but cover several cells. The longitudinal ridges may be partly the result of contraction on drying. Testa tending to break along the digitate outlines. A more conspicuous rounded longitudinal ridge marks the raphe. Testa about 0·15 mm. thick in section. The embryotega is convex externally with large median rimmed micropyle. It is formed of rectangular or square thick walled cells which sometimes appear slightly sinuous. They are about 0·05 mm. in diameter. Tegmen thin, translucent, yellowish finely striate. Dimensions : Length, 1·25 to 2·5 mm. ; breadth, 1 to 2 mm.

REMARKS. The Upper Headon specimens fall approximately within the range of size of *Brasenia spinosa* from the Lower Headon of Hordle, a few seeds of which are here shown for comparison (Pl. 30, figs. 64, 65, 67–69). Those in figs. 67–69 are small specimens with coarse tubercles which were originally separated as a distinct species *B. antiqua*. However, it later appeared that the two varieties, one with spiny tubercles, the other with short thick tubercles graded into one another so that they could not be separated (Chandler, 1961*b* : 117). On the whole the Lower Headon seeds tend to be smaller. Thus dimensions of *B. spinosa* from Hordle were originally given as 1·5 by 1·5 mm. and of *B. antiqua* as 1 by 0·75 to 1 mm. Recent measurements of Hordle seeds give length, 1 to 2·25 mm. ; breadth, 2·25 by 2·25 mm. In addition to figured material there are V.43846–47, V.43849 from between Brambles and Linstone Chines and V.43848 from south of Linstone Chine.

Genus ***NYMPHAEA*** (Tourn.) L.

Nymphaea sp.

(Pl. 29, figs. 60, 61)

DESCRIPTION. *Seed :* Ellipsoid, very slightly truncate at the hilar end where the burst aperture for a small embryotega can be seen. Embryotega present but obscure in V.43850, the aperture not more than 0·3 to 0·4 mm. in diameter. Anatropous, the longitudinal raphe forming a slight ridge from base to apex. Surface of seed obscurely longitudinally ridged, the ridges lying along the junctions of longitudinal rows of digitate cells with interlocking claws which may be lobed or forked at their extremities. These cells, which are also aligned in distinct transverse rows, are often transversely elongate but sometimes equiaxial. They are about 0·05 to 0·15 mm. in diameter. The hilar end of the seed around the embryotegal aperture has distinct radially arranged crumples. A few fine sharply pointed tubercles are seen along the ridges closely adpressed to the surface. Length of seed, 2·75 mm. ; breadth, 1·25 to 1·5 mm.

REMARKS. The two figured specimens are the actual carbonaceous seeds themselves. An internal cast in pyrites of a third specimen has now decayed. On it the regularly arranged digitate cells were formerly beautifully preserved as impressions with shorter, more rounded swollen-ended digitations. The whole surface of the pyrites cast also showed rounded cells about 0·008 mm. in diameter, perhaps the replacement of albumen cells. The elliptical aperture from which the embryotega had disappeared was represented by an impression with maximum diameter of about 0·03 mm. There is some resemblance to *Brasenia oblonga* Chandler from the Lower Headon of Hordle but these Colwell seeds have a more ellipsoid form, larger size and less regular tubercles. Form and arrangement of the surface cells appear to ally them with *Nymphaea*.

Family DROSERACEAE

Genus ***ALDROVANDA*** (Monti) L.

Aldrovanda ovata (Chandler)

(Pl. 30, figs. 70, 71)

1961*b* *Aldrovanda ovata* (Chandler) : Chandler, p. 119, pl. 26, figs. 53–55. See also for earlier references.

Description. *Seed :* Oburceolate with a narrow neck about one-sixth to one-seventh of the length of the whole seed, closed by a circular plug having a central thick short mucro from which the small convex equiaxial cells of its outer surface radiate. Anatropous with conspicuous longitudinal raphe ridge terminating in a marked mucro at the apex over the chalaza at one end and in the basal hilum on the margin of the neck at the other. Surface black, shining, testa formed of two coats, an outer coat 0·05 to 0·1 mm. thick, of radially arranged cells as seen in section whose slightly inflated outer ends give rise to flat or scarcely convex equiaxial cells about 0·001mm. in diameter on the external surface. On the internal surface there are cells about 0·002 to 0·003mm. in diameter. An inner coat, 0·15 mm. thick is formed by a single layer of radially arranged prismatic cells about 0·02 to 0·05 mm. in diameter. Dimensions of several seeds : 1) Length, 1·75 mm. ; breadth, 1·35 mm. ; length of neck, 0·25 mm. 2) Length, 1·76 mm. ; breadth, 1·4 mm. ; length of neck, 0·3 mm. 3) Length, 1·9 mm. ; breadth, 1·25 mm. ; length of neck, 0·25 mm. 4) Length, 2 mm. ; breadth, 1·25 mm. ; length of neck 0·25 mm. 5) Length, 1·75 mm. ; breadth, 1·25 mm. ; length of neck, 0·25 mm. 6) Length, 2 mm. ; breadth, 1·25 mm. ; length of neck about 0·3 mm. Average length of seeds, 1·83 mm. ; average breadth, 1·28 mm.

Remarks and Affinities. About a dozen seeds and some fragments. They agree in every respect with *Aldrovanda ovata* (Chandler) from the Lower Headon of Hordle (Chandler, 1925 : 22, pl. 3, fig. 3*a*, *b* ; Reid & Chandler, 1926 : 113, pl. 4, figs. 24–26) in their large size, conspicuous apical mucro and marked raphe ridge, relatively long neck and smooth surface and thick testa, the two coats of which together measure nearly a quarter of the diameter of the seed. The characters which distinguish this species from *A. intermedia* Reid & Chandler (Bembridge and Hempstead) and *A. vesiculosa* L. (Recent) were discussed by Reid & Chandler (1926 : 111–113). In addition to figured material there is V.43855, all from below the sewer pipe, Linstone Chine, also V.43856–57 from between Brambles and Linstone Chines, and V.43858 in folded beds close to Fort Victoria boundary fence.

Family ROSACEAE

Genus *RUBUS* (Tourn.) L.

? *Rubus microspermus* C. & E. M. Reid

(Pl. 30, figs. 72, 73)

1910 *Rubus microspermum* C. & E. M. Reid, p. 169, pl. 15, figs, 13–17.
1957 *Rubus microspermus* C. & E. M. Reid : Chandler, p. 101, p. 14, figs. 100–109.

DESCRIPTION. *Endocarp :* Laterally compressed, semicircular to narrow-ovate in outline ; ventral margin concave, straight or slightly convex, dorsal margin semicircular or markedly convex. Base rounded. Apex sometimes narrower than base, sometimes curved towards the ventral side, margin rimmed all round. Surface reticulate with conspicuous angular pits separated (in unworn specimens) by clearly defined ridges. Dimensions of several endocarps are as follows : 1) Length, 2·9 mm. when moist, 2·85 mm. after drying and shrinkage ; breadth, 1·25 mm (moist), 1·2 mm. (dry). 2) Length, 2·25 mm. (moist), 2 mm. (dry); breadth, 1·3 mm. (moist), 1·25 mm. (dry). 3) Length of much abraded hooked endocarp, 2·1 mm. ; breadth, 1·1 mm.

REMARKS. These endocarps agree, so far as they are known, with *Rubus microspermus* from Bovey Tracey but they appear to be larger on the whole. They are less narrow and pointed at the apex than *R. acutiformis* from the Dorset Pipe-clay Series at Studland, the Bournemouth Freshwater Beds of Branksome Dene and the Lower Headon of Hordle. *R. acutiformis*, dry, measures 1·55 by 1·2 mm. ; 2 by 1·25 mm. ; 1·5 by 1 mm. The dimensions when wet were 2 to 2·25 by 1·3 mm. Typical Bovey specimens of *R. microspermus* dry measure 2·1 by 1·25 mm. ; 2·25 by 1 mm. ; 2 by 1·25 mm.

In the absence of a larger range of material showing variations of size and form the Colwell species is referred provisionally only to *R. microspermus*. In addition to the figured specimens from below the sewer trench, Linstone Chine, there are endocarps V.43861 from beds between Brambles and Linstone Chines, only one now complete.

Family RUTACEAE

Genus *ZANTHOXYLUM* Linnaeus

Zanthoxylum hordwellense Chandler

(Pl. 30, figs. 74–80)

1925 *Zanthoxylon* cf. *ailanthoides* Sieb. & Zucc. Chandler, p. 26, pl. 4, fig. 3*a*, *b*; text-fig. 9.
1961*b* *Zanthoxylum hordwellense* Chandler, p. 123, pl. 26, figs. 63, 64.

DESCRIPTION. *Seed :* Semianatropous, approximately semicircular or gibbous to subcircular in outline with ventral margin very slightly convex, dorsal rounded. Somewhat flattened laterally so as to give a sublenticular outline in transverse section. Ventral margin with an elongate narrow triangular depressed hilar scar occupying from half to three-quarters of the length in the upper part. There is a tendency for it to be somewhat asymmetric and slightly curved. Hilar aperture at the base of this scar leading into raphe canal which extends within to the internal chalaza and causes the slight prominence in the lower part of the ventral margin. Chalaza large about 0·3 mm. in diameter, lying on the ventral side of the longest axis of the seed. Testa thick, concentric wrinkles present but somewhat obscured by abrasion, formed of equiaxial cells arranged so as to give a columnar appearance in section. Cells on external surface crenulate or finely sinuous. On the internal surface they are about 0·016 mm. in diameter. Tegmen or inner integument thin, papery, semi-translucent, light brown in colour, formed of equiaxial cells 0·01 to 0·025 mm. in diameter smallest at the chalaza and at the opposite pole of the seed. Typical seed measurements: 1) Length, 3·5 mm.; breadth, 3 mm.; thickness, 2·75 mm. Length of hilar scar, 3 mm. 2) Length, 3 mm.; breadth, 2·75 mm. 3) Length, 4·5 mm.; breadth, 3 mm.; thickness, 2·75 mm. Length of hilar scar, 2·5 mm. Seed somewhat distorted in growth. 4) Length, 2·25 mm.; breadth, 2·25 mm. 5) Length, 3·25 mm.; breadth, 3·25 mm.

REMARKS. The seeds are not uncommon between Brambles and Linstone Chines. In addition to figured material from this site there are also V.43866–67 from folded beds close to the Fort Victoria boundary. The last mentioned apparently an internal cast with thick testa gone, perhaps immature. They agree in size and characters with the specimens from the Lower Headon of Hordle, but are generally more abraded so that the superficial wrinkles are less conspicuous although still visible (Pl. 30, figs. 74, 77, 78) and the fine cells of the epicarp are not seen for the same reason. The raphe is exposed in longitudinal section and the chalaza in broken seeds. A peculiar feature is the heavy pyritization in the form of a fine soft amorphous powder or mud which does not retain clear cell impressions as it readily smears. In this respect the Colwell seeds are less well preserved than the Hordle ones and are even more liable to decay.

Family THEACEAE

Section TAONABEAE

Genus ***HORDWELLIA*** Chandler, 1960: 228

Hordwellia crassisperma (Chandler)

(Pl. 30, figs. 81–85)

1961*b* *Hordwellia crassisperma* (Chandler): Chandler, p. 140. See also for earlier references.
1962 *Hordwellia crassisperma* (Chandler): Chandler, p. 112, pl. 17, figs. 8–61.

DESCRIPTION. *Fruit:* Inferior, subglobular but now much distorted dorsiventrally-oblique and flattened. Showing a small raised rim representing the persistent perianth base with three-rayed ridge inside it indicating three locules. Sepals not preserved. Surface of fruit finely pitted. Diameter about 1·25 by 1·75 mm.

Seed: Subovate to cuneate in outline, truncate at the hilar end, hilum and micropyle adjacent on the truncation as described in 1962 and earlier, varying considerably in form and size as is typical for this species. Surface pitted as described in earlier accounts, pits and inner part of wall made up of fine equiaxial cells. Typical seed measurements are as follows: 1) Length, 1·5 mm.; breadth, 1·25 mm. 2) Length, 1·85 mm. ; breadth, 1 mm. 3) Length, 1·5 mm. ; breadth, 1 mm. 4) Length, 1·25 mm. ; breadth, 1 mm. 5) Length, 1·4 mm. ; breadth, 0·8 mm. 6) Length, 1·25 mm. ; breadth, 0·8 mm. 7) Length, 1 mm. ; breadth, 0·75 mm.

REMARKS. For the geological range hitherto recorded for this species see Chandler (1962). The seed from the Upper Headon figured in Pl. 30, fig. 83 is slightly different in appearance from the normal, the external pits being unusually regular and symmetrically arranged probably due to the fact that it is preserved in pyrites and the pit walls are therefore rigid.

Family LYTHRACEAE

Genus ***DECODON*** J. F. Gmel.

Decodon vectensis n.sp.

(Pl. 30, figs. 86–90 ; Pl. 31, figs. 91–98)

DIAGNOSIS. Seed triangular pyramidal, edges sharply angled. Dorsal surface sharply angled over the raphe. Outer surface of germination valve somewhat concave. Outer woody compact coat of testa much thinner than the inner woody coat, middle spongy coat thicker than either. Length of seeds, 1 to 1·2 mm. ; breadth parallel with valve, 0·55 to 0·75 mm. ; dorsiventral thickness, 0·5 to 0·8 mm.

HOLOTYPE. V.43873.

DESCRIPTION. *Seed :* Inverted triangular pyramidal in shape with sharply angled edges, apex broad, sometimes but not invariably sloping away from the valve and meeting the sides at a sharp angle. Base often slightly stipitate. Dorsal side sharply angled the angle forming a conspicuous ridge associated with the raphe. Outlines of lateral margins concave or straight. Ventral side with a narrow triangular or obovate germination valve with its surface somewhat concave both in a longitudinal and transverse direction, confluent with the testa of the seed at its broad upper end and never separating from it in this region. It extends to the base of the seed below and gives rise to the stipitation. Outer surface of valve ornamented by about twelve narrow longitudinal grooves each with a line of pits (not clear in the figures). Micropyle sub-basal or basal between the pointed end of the valve and base of seed body. Hilum basal leading into dorsal raphe canal. Chalaza a large apical black circular scar about 0·11 mm. in diameter inside the seed cavity. Outer epidermal layer of testa abraded. Main thickness of testa showing three regions : an inner somewhat woody compact coat about 0·027 mm. thick near the apex, an outer similar but much thinner coat and a middle coat thicker than either of the other two (about 0·054 mm. thick where it could be measured) formed by a mass of spongy cells. Tegmen thin, longitudinally striate. Length of seeds usually about 1 mm., rarely as much as 1·2 mm. ; dorsiventral thickness of several seeds 0·5, 0·66, 0·75, 0·8 and 1 mm. respectively. Breadth, from side to side (i.e. parallel with the valve) 0·55, 0·7, 0·75 and 0·66 mm. in four seeds.

REMARKS. Sixteen seeds from the beds between Brambles and Linstone Chines. V.43880 (not figured) includes nine seeds. This species is very small in comparison with the living *Decodon verticillatus* or the fossils *D. globosus* E. M. Reid and

D. gibbosus E. M. Reid. The seeds are also much more sharply angled, a feature seen in mature seeds with well developed seed cavities as well as in immature specimens. In the dorsiventral depth they are most comparable with *D. gibbosus* but they do not resemble it closely in other respects. In the greater thickness of the internal woody layer they approach *D. verticillatus*. The differences indicated although slight appear to justify specific designation and the name *Decodon vectensis* has been given.

Genus ***MICRODIPTERA*** Chandler, 1957 : 107

? ***Microdiptera parva*** Chandler

(Pl. 31, figs. 99–107)

1957 *Microdiptera parva* Chandler, p. 107, pl. 15, figs. 133–149 ; text-fig. 2.
1961*b* *Microdiptera parva* Chandler : Chandler, p. 141, pl. 29, figs. 116, 117.
Microdiptera parva Chandler : Chandler (in press), p. 119, pl. 19, figs. 30–35.

DESCRIPTION. *Seed :* Usually much compressed dorsiventrally, subtriangular, oval, quadrangular, pentagonal or irregular in outline, differentiated into a median elongate-ellipsoidal body flanked by thin lateral wings, more or less convex on the dorsal surface. Raphe prominent, linear, longitudinal, median on the ventral face of the broad elongate seed-body, indicated by longitudinally striate cells. It is flanked by two deep concavities which are partly overlapped by a flap of wing. Hilum marginal. Germination by an elongate oval operculum or plug extending from the base of the dorsal face to about half to four-fifths of the length of the seed from the apex. Germination starts at the lower end of this plug where the micropyle is situated but the whole plug eventually separates completely from the seed along a finished suture. Surface of plug convex, sometimes markedly so in seeds where a pyrites cast of the seed cavity is preserved. Testa shining superficially due to a layer of angular cells of variable outline. Cells over the operculum arranged in about five to eight longitudinal rows which are 0·05 mm. broad. These cells are equiaxial or broader than long. Lining of seed of equiaxial regular small cells, best seen as impressions on the pyrites seed-cast. Similar cells are seen immediately underlying the equiaxial coarse cells of the operculum. Dimensions of seeds : 1) Length, 1·1 mm. ; breadth, 1·2 mm. 2) Length, 1·1 mm. ; breadth, 1·6 mm. 3) Length, 1·25 mm. ; breadth, 1·1 mm. 4) Length, 1 mm. ; breadth, 1·25 mm. 5) Length, 1 mm. ; breadth, 1·1 mm. 6) Length, 0·9 mm. ; breadth, 1·75 mm.

REMARKS. The relationship to Lythraceae has been discussed earlier (Chandler, 1957 : 108). The species resembles *Microdiptera parva* closely and is appreciably smaller than *M. major* (Chandler, in press). In some degree the Upper Headon specimens are abnormal. The majority have all cavities filled with pyrites which has distended them and ruptured the thin carbonaceous walls. Later these walls have flaked away wholly or in part leaving conspicuously convex casts of the opercula or seed-bodies which form therefore unusually striking features. A few unpyritized seeds were found which do not show these distinct convexities, thus indicating that they are due to preservation and are not of specific significance. The seeds are therefore referred provisionally to *Microdiptera parva* although attention is called to the unusually long plug in some specimens which may extend to the apex of the seed.

There are also the following abnormal features. The seed in Pl. 31, figs. 105, 106 has a particularly well preserved surface. It shows longitudinal striae on both sides of the body ventrally and irregular striae mostly diverging from the body over most of the wing surface. In this specimen the plug extends almost to the top of the seed and it is swollen and fusiform. On the ventral surface there is a deep narrow longitudinal groove on each side of the body which is broad and somewhat fusiform. In addition to figured specimens there is V.43885. All are from beds between Brambles and Linstone Chines.

One seed, now decayed, was peculiarly thick from back to front with large swollen body and small much reflexed wings causing the dorsal surface to be conspicuously convex. Its operculum extended almost the whole length of the dorsal surface. The seed-body on the ventral surface appeared broad and inflated, broadening upwards and extending throughout the length of the seed.

Family CAPRIFOLIACEAE

Genus ***SAMBUCUS*** (Tourn.) L.

Sambucus colwellensis n.sp.

(Pl. 31, figs. 108–113)

DIAGNOSIS. Seeds normally 1·5 to 1·75 mm. long rarely smaller. Furrows between sinuous transverse ridges deeper in this species than in *Sambucus parvula* from Hordle.

HOLOTYPE. V.43886.

DESCRIPTION. *Seed:* Obovate or elongate-obovate in outline, compressed, frequently concavo-convex at least in fossilization, anatropous. Micropyle and hilum terminal on the ventral face marked by a tiny slit-like aperture at the pointed end, raphe median longitudinal marked sometimes by a slight angle. Surface ornamented with about ten or more sinuous transverse sometimes interrupted ridges with deep furrows between them. Concave ventral surface with a distinct marginal rim. Testa formed externally of small equiaxial cells about 0·016 mm. in diameter and internally of larger ones. Germination by marginal splitting into two valves. Length of seed normally about 1·5 to 1·75 mm.; breadth commonly 0·75 to 1 mm. The smallest seed measured was 1·2 mm. long, 0·85 mm. broad. The broadest seed measured was 1·6 mm. long, 1·25 mm. broad. Several seeds 1·25 mm. long were seen which varied from 0·75 to 1 mm. in breadth.

REMARKS. Numerous seeds, somewhat similar to *Sambucus parvula* from the Lower Headon of Hordle in the surface ornamentation, but readily distinguished from that species by their considerably greater size. In *S. parvula* a length of 1·5 mm. is rare. The two species as they lie side by side can be distinguished at a glance by this character. The furrows between the transverse sinuous ridges also tend to be deeper in the Colwell than in the Hordle seeds. The Colwell seeds therefore appear to merit a distinct specific name, *Sambucus colwellensis*. As they are heavily pyritized shrinkage has no doubt been reduced to a minimum and the sizes quoted are in all probability the true sizes of the living seed. The specimens were also compared with

Sambucus mudensis from the Highcliff Sands, Cliff End, Mudeford (Chandler, in press), but that species has seeds as much larger than *S. colwellensis* as those of *S. colwellensis* are than seeds of *S. parvula*. *Sambucus* seeds are among the commonest of the Upper Headon plant remains and can be found all along the section suggesting a line of elder trees or elder scrub overhanging the river or marsh. The figured specimens were collected below the sewer at Linstone Chine and between Brambles and Linstone Chines. In addition there is V.43892 from the last locality and V.43893 from folded beds close to Fort Victoria boundary fence.

Family EPACRIDACEAE

Genus ***EPACRIDICARPUM*** Chandler, 1960 : 214

Epacridicarpum headonense Chandler

(Pl. 31, figs. 114–116)

1960 *Epacridicarpum headonense* Chandler, p. 234, pl. 34, figs. 146, 147.
1961*b* *Epacridicarpum headonense* Chandler : Chandler, p. 146, pl. 29, figs. 134–137.
Epacridicarpum headonense Chandler : Chandler (in press), p. 126, pl. 21, figs. 2–5 ; text-fig. 23.

DESCRIPTION. *Fruit :* A subhemispherical or oblate-sphaeroidal five-loculed loculicidal capsule. Upper surface somewhat flattened, lower convex (stipitation not preserved), axis stout, fibrous, flat-topped. Surface with irregular pits. Walls thick ; inner layers of elongate longitudinally aligned cells which diverge from the subapical axile placentae. Dimensions of several fruits : 1) Diameter, 1·6 mm. ; dorsiventral thickness, 0·8 mm. 2) Diameter, 1·3 mm. ; dorsiventral thickness, 1 mm. 3) Diameter, 1·75 mm. ; dorsiventral thickness, 1·25 mm.

REMARK. The specimen has now split loculicidally into its component valves. When first seen and photographed (Pl. 31, fig. 114) these hung together but had contracted near the axis making oval apertures prolonged as splits along the lines of the locules. The decay of the axis has in some specimens left a gap at the apex and an empty canal below is now filled with sand. In addition to the figured material there is V.43987, all from between Brambles and Linstone Chines. The specimens are identical with the Hordle species which is known also from the Lower Bartonian of Barton and the Highcliff Sands of Mudeford.

Epacridicarpum colwellense n.sp.

(Pl. 31, figs. 117–119)

DIAGNOSIS. Fruit five-carpelled, subsphaeroidal but somewhat depressed dorsiventrally. External surface finely and evenly pitted, the upstanding walls of the pits producing rugosities. Sharply angled over the locules with deep concavities over the septa. Transverse diameter about 1·25 to 1·5 mm. Dorsiventral diameter, 0·75 to 1 mm.

HOLOTYPE. V.43898.

DESCRIPTION. *Fruit :* Syncarpous, five-carpelled, subsphaeroidal but somewhat depressed so that it is broader than long, having five longitudinal angles so that the outline as seen from above or below is somewhat star-shaped with deep concavities between the angles. The angles overlie the locules. Dehiscence loculicidal. Axis thick and fibrous. Locules with elongate cells diverging from the inner apical angle. External surface somewhat rough, finely and more or less evenly pitted, the raised walls of the pits producing the rugosities. Placentation probably axile at the apical angle of the locules from which the cells diverge. No seeds seen. Dimensions: 1) Maximum transverse diameter, 1·5 mm.; dorsiventral thickness (crushed and therefore reduced), 0·75 mm. 2) Transverse diameter, 1·25 mm.; dorsiventral thickness (scarcely crushed), 0·75 mm. 3) Transverse diameter, 1·24 mm.; dorsiventral thickness, 1 mm.

REMARKS. The specimens are mostly obliquely distorted. They differ from *Epacridicarpum mudense* Chandler (1960: 214, 235, pl. 31, fig. 57; pl. 34, figs. 148–150), another somewhat angled species in the relatively smooth surface with fine pitting and the more marked angles over the locules with deep depressions over the septa. In addition to figured material there is V.43901 including several fruits. All are from beds between Brambles and Linstone Chines.

Family ?

Genus ***RHAMNOSPERMUM*** Chandler, 1925: 30

Rhamnospermum bilobatum Chandler

1962 *Rhamnospermum bilobatum* Chandler: Chandler, p. 146, pl. 23, figs. 18–38; pl. 24, figs. 1–9. See also for earlier references.

The species is common. Specimens are frequently much crushed, distorted and shrivelled. Often only the inner semitranslucent coat is preserved. A unique specimen from the Upper Headon apparently attached to a stalk, possibly provided with a ring of calyx lobes, is described by Chandler (1962: 146, pl. 24, figs. 8, 9). Typical measurements of Upper Headon material are length, 2·75 to 3·5 mm.; breadth, 3 mm.

INCERTAE SEDIS

Carpolithus colwellensis n.sp.

(Pl. 32, figs. 120–126)

DESCRIPTION. *Fruit:* Inferior, one-loculed, tapering towards the apex, the greatest breadth being at or just above the base, having three longitudinal facets, one broad and flat, occupying half of the circumference, the other two narrower meeting the broader facet to form marginal angles, and one another to form a median longitudinal angle on the opposite side of the fruit to the broad facet. Along all three longitudinal angles a furrow can be seen down which splitting may occur starting at the apex. Apex with three small short or broad patent triangular perianth segments one opposite each facet. Externally the segments show longitudinal puckering at their tips. Base of fruit (usually broken) in the best preserved specimen somewhat excavated (Pl. 32, figs. 122, 123), a slight marginal ridge around the excavation delimiting an ellipsoidal or oval depression with a small median scar. Surface rough with inconspicuous tubercles arranged in longitudinal rows. The tubercles are slightly elongate longitudinally and about 0·016 mm. broad. There are also superficial rectangular inflated cells producing a tubercled effect. Tubercles and cells together give a " rippled " surface. When abraded a finer surface is exposed with longitudinal lines of cells only about 0·008 mm. broad. In one specimen a valve has come away along two of the ridges showing the single locule and a columnar wall built of small rectangular cells radially aligned. Dimensions: 1) Length, 2·5 mm.; breadth, 1 mm.; thickness, 0·5 mm. 2) Length, 2 mm.; breadth, 0·75 mm. 3) Length (with incomplete apex), 2·25 mm.; breadth, 1·25 mm.; thickness, 0·5 mm. 4) Length, 2 mm.; breadth, 0·75 mm.; thickness, 0·5 mm.

REMARKS. The relationship of these much pyritized fruits has so far eluded discovery.

Carpolithus sp.

(Pl. 32, figs. 127–130; Text-fig. 2)

DESCRIPTION. Part of a capsule ? Subcircular in outline, slightly narrowed to one end which bears a straight, obliquely directed pointed spine-like process arising at about 0·5 mm. from the margin as seen in profile (Text-fig. 2). The main part of the specimen, when uncrushed, is inflated and almost hemispherical on the outer surface, deeply concave on the inner which has a finished suture-like flat edge. A collapsed specimen shows that the " spine" is hollow although there is no evidence of an aperture leading into it on the concave surface of the organ. Wall with two definite layers, an outer with coarse cells at right angles to the surface and an inner of equiaxial cells. Between the two layers the thickness appears to be of cells parallel with the inner margin but all are much obscured by sand-pitting. Length of body of uncrushed specimen, 3 mm. Length of body and spine, 4·75 mm.; breath, 3·25 mm. Length of crushed specimen, 3·1 mm. including spine; breadth, 3·25 mm. In addition to figured material there are two imperfect specimens (V.43911) of which one shows the spine. The nature of these bodies is obscure but they may represent a valve of a capsule. All are from between Brambles and Linstone Chines.

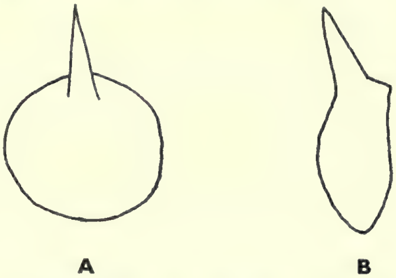

FIG. 2. *Carpolithus* sp. A, Inflated external surface of ? valve of capsule showing spine-like process. B, Same, side view.

Carpolithus spp.

(Pl. 32, figs. 131, 132)

Two ovoid seeds (now compressed in fossilization). In one (Pl. 32, fig. 132) the broader end is very slightly flattened, the opposite narrowed but pointed. Surface shining, pitted, the pits about 0·013mm. in diameter. Length, 1 mm. ; breadth, 0·7 mm. The second (Pl. 32, fig. 131) is similar in shape but not flattened at either end. Its surface is formed of small equiaxial polygonal cells. Length, 1·25 mm. ; breadth, reduced by folding, 0·75 mm. Both show little that is distinctive. They do not appear to be identical. Both are from beds between Brambles and Linstone Chines.

Carpolithus sp.

(Pl. 32, fig. 133)

DESCRIPTION. *Fruit* (or seed ?) : Elongate-oval in outline, narrowed to a point at one end (base ?), truncate at the opposite end where there is a subcircular or elliptical disc which may have borne a perianth or pappus. The specimen is somewhat compressed. The disc appears to be subdivided by a slight constriction at right angles to its maximum diameter giving it a slightly bilobed effect. At the opposite extremity of the fruit the cells converge suggesting an organ situated here. Surface rather rough formed of rounded cells about 0·008 mm. in diameter. Inner integument shining, semitranslucent, showing longitudinal rows of cells, the rows about 0·03 mm. broad, the cells transversely aligned producing transverse striation of the ridges where adjacent rows are contiguous. Length of specimen, 1·75 mm. ; breadth, 0·75 mm.

REMARKS. The single specimen (V.43914) is from beds between Brambles and Linstone Chines. The outer integument has flaked away showing the shining inner coat in patches. The specimen, with a disc at the apex, recalls *Typha* seeds but the cell structure is unlike that of *Typha* nor is its form as fusiform-truncate. It is appreciably larger than seeds of *Typha latissima* (length, 0·9 to 1·1 mm.). Its relationship has not been discovered.

Carpolithus sp.

(Pl. 33, figs. 140, 141)

DESCRIPTION. *Fruit :* Elongate-oval, somewhat truncate obliquely at one end, pointed at the other having a large scar (of attachment ?) at the truncation. More or less bisymmetric, somewhat compressed at right angles to the plane of symmetry in which it splits. External surface with a few inconspicuous broad longitudinal ridges, fine pits and small shining inflated cells. Locule lining having elongate longitudinally aligned cells with finely toothed walls 0·025 mm. broad. Length of fruit, 3·5 mm. ; breadth, 2 mm. V.43915, now much broken, from beds between Brambles and Linstone Chines. Relationship unknown.

Unknown leaf

(Pl. 32, figs. 134–139)

DESCRIPTION. Four small fragments of a long narrow leaf with pinnate rounded lobes on each side of a stout midrib. Fragments stiff, coriaceous, convex on the upper surface (Pl. 32, figs. 134, 136, 138). Margins of lobes sharply recurved onto the lower surface where they appear revolute and rounded making a pouch over the concave lower surface of each lobe (Pl. 32, fig. 137). Midrib stout, prominent on the lower surface (Pl. 32, figs. 135, 137, 139), sunk in a narrow furrow on the upper surface (Pl. 32, figs. 134, 138). Other nerves indistinguishable but the pinnule or leaf lobes are separated from one another by deep curved furrows on the upper surface (Pl. 32, figs. 134, 136). Cells of upper surface straight-sided not digitate, angular equiaxial near the margin, somewhat elongate transversely to the length of the leaf near the midrib. Cells on lower surface longitudinally aligned and elongate over the midrib. One fragment representing the basal end narrowed downwards towards the stalk (Pl. 32, figs. 138, 139) was about 2 mm. long, 0·75 mm. broad and its lobes were only about 0·5 mm. long and had diminished at the lower end so as to have almost disappeared. V. 43916 represents the remains of this specimen. The largest fragment, now decayed, (Pl. 32, figs. 134, 135) was 3 mm. long, 1 mm. broad, the midrib on its lower surface being 0·25 mm. broad with pinnule lobes about 0·5 mm. long. A tiny fragment (Pl. 32, figs. 136, 137) must have been from a much larger leaf. Only three lobes were preserved on one side of the midrib and one on the other. The stout convex midrib measured almost 1 mm. in breadth on the lower surface and was flanked on each side by deep furrows representing the true lower surface exposed between the midrib and the revolute rounded upper margins of the pinnule lobes. In this larger specimen the lobes were from 1 to 1·2 mm. long. Only a fragment of one lobe (V.43917) remains. A fourth fragment (V.43918) is distorted and folded lengthwise and upwards upon itself along the rounded prominent midrib. It shows three rounded inflated lobes on one side and two on the other. Length of midrib, 2·5 mm. ; breadth of specimen as folded, 1 mm. Length of lobes, 0·75 mm.

REMARKS. The superficial appearance of this specimen resembles *Gleichenia*, but the straight-sided cells do not appear to support this relationship. It has not been possible to discover the affinities of these fragments found in a tiny film or pocket of vegetation in sandy beds between Brambles and Linstone Chines in which *Anemia colwellensis* was also discovered.

b) *The Osborne Beds*

Localities as stated under descriptions. Preserved in Museums stated.

PTERIDOPHYTA

Order FILICALES

Family POLYPODIACEAE

Genus ***ACROSTICHUM*** Linnaeus

Acrostichum lanzaeanum (Visiani)

(Pl. 33, fig. 142 ; Text-fig. 3)

1961*b* *Acrostichum lanzaeanum* (Visiani) : Chandler, p. 101, pl. 24, fig. 2. See also for earlier references.

Two small fragments of pinnule impression (No. 379 about 7 by 7 mm. ; No. 377 length, 17 mm. ; breadth, 15 mm.) have been found at Cliff End at the northern end of Colwell Bay. They were orginally covered by carbonaceous substance but this has now almost entirely chipped away exposing the underlying impression. The highly characteristic reticulate nervation is seen. The fragments are readily recognizable on account of the better preserved material so frequently found at older Eocene horizons. Well preserved pinnules are also known from the Bembridge Beds. Both specimens were collected by Clement Reid and Henry Keeping and are preserved in the Geological Survey Museum. In the case of specimen 379 the edge of the specimen is broken and chipped away (Text-fig. 3). In 377 (Pl. 33, fig. 142) the fragment lay to one side of the midrib. The actual midrib and margin are missing.

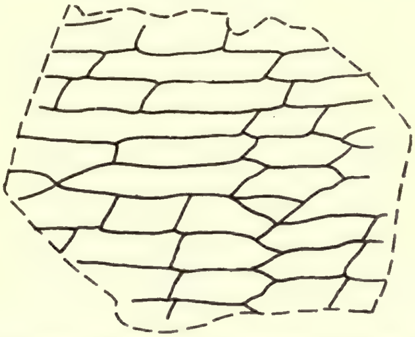

FIG. 3. *Acrostichum lanzaeanum* (Visiani). Fragment of leaf impression broken all round its edges.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

? *Stratiotes neglectus* Chandler

(Pl. 33, figs. 143–146)

1923 *Stratiotes neglectus* Chandler, p. 126, pl. 5, figs. 4, 27, 28 ; pl. 6, fig. 24.
1926 *Stratiotes neglectus* Chandler : Reid & Chandler, p. 74, pl. 4, figs. 13, 14.

DESCRIPTION. *Seed :* Suboval or oblong, hooked at the base, much flattened ; keel moderately broad but thin and sometimes broken causing the seed to appear sigmoidal (Pl. 33, figs. 144, 146), not continued round the base but merging into the collar which is relatively large and prominent, rounded and smooth or slightly rough ; testa thin, woody with irregular longitudinal tubercles often coalescing to form longitudinal ridges rarely continued onto the collar, sharp and thin when well preserved. Surface pitting fairly coarse ; micropyle basal oblique ; hilum dorsal near the base ; raphe marginal from the hilum upwards for at least half its length, thereafter diagonal entering the seed cavity at the apex. Width of the testa outside the diagonal portion less than that inside in the only specimens where it is exposed. Digitate cells of interior of keel (seen in one specimen only) tortuous near the base. Length of seeds about 2·9 to 3·5 mm. ; breadth about 1·6 to 2 mm., much flattened.

REMARKS. The seeds from the Osborne Beds of Osborne are clearly immature or abortive, battered and much crushed, several have broken in part along the line of the raphe giving a spuriously sigmoidal outline. Their characters so far as they could be ascertained suggest *Stratiotes neglectus*, but in view of the condition of these specimens the determination is regarded as provisional. In addition to four figured seeds or valves there are twenty-one others (V.43927).

Class DICOTYLEDONES

Family NYMPHAEACEAE

Genus ***NELUMBIUM*** Juss.

Nelumbium buchi Ettingshausen

1862 *Nelumbium Buchii* Ettingshausen : Heer, p. 374, pl. 18, fig. 19.
1888 *Nelumbium Buchii* Ettingshausen : Gardner, pp. 417, 423, pl. 4.

A characteristic but poorly preserved fragment of a rhizome of the type attributed by Heer and by Gardner to *Nelumbium buchi* Ettingshausen (see p. 376) is in the Geological Survey Museum (No. 360 XX 6/16a) from Cliff End near Colwell Bay.

INCERTAE SEDIS

Genus ***DICOTYLOPHYLLUM*** Saporta emend. Bandulska, 1923 : 244

Dicotylophyllum pinnatifidum Reid & Chandler

(Pl. 33, fig. 147 ; Text-fig. 4)

1926 *Dicotylophyllum pinnatifidum* Reid & Chandler, p. 151, pl. 10, figs. 8–12.

DESCRIPTION. *Leaf :* Represented by a tiny carbonaceous fragment at the tip of a pinnatifid leaf with about six rounded segments. The sunk midrib is well shown. Secondary nerves, alternate or opposite, arise from it at a wide angle, one running towards the tip of each segment. Each nerve gives off a reflexed branch which passes towards the sinus below and, perhaps owing to curling of the leaf margin, appears to pass into the sinus. Margins of segments entire so far as seen but not sufficiently well preserved to show the hyaline border described in the Bembridge specimens. The fragment is only about 6 mm. long and its maximum breadth is 2·25 mm. From the Osborne Beds of Cliff End near Colwell Bay. No. 376 Geological Survey Museum.

There is no further light on the identity of the species but attention is called to a resemblance it bears to a compound leaf, or stem bearing several leaves, reproduced by Krystofovich (1957 : 391, text-fig. 383) after Korovin (1949) who had named it *Palibinia densifolia* and referred it to the Proteaceae. The figure shows a leaf of similar form and there is some suggestion of a hyaline margin, but the branching of the nerves is not clear and without comparison of actual material it is not possible to say whether the two are identical. *Palibinia densifolia* is also described and figured by Vacdlevcka in 1957 (*in* Krystofovich, 1957 : 143, pl. 4, figs. 1–5 where references are given to papers in 1932, 1934).

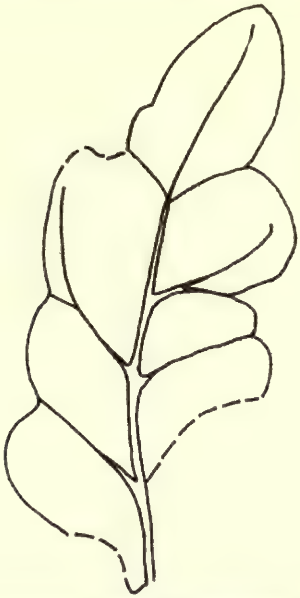

FIG. 4. *Dicotylophyllum pinnatifidum* Reid & Chandler. Diagram showing outline of leaf fragment and nerves.

(c) *Bembridge Beds*

Localities of new material as indicated in text.

PTERIDOPHYTA

Order FILICALES

Family SCHIZAEACEAE

Genus ***ANEMIA*** Swartz

Anemia sp. (**? *A. colwellensis*** Chandler)

1926 Filix incertae sedis, sp. 5 Reid & Chandler, p. 39, pl. 1, figs. 10, 11.
1955 *Anemia* sp.3 Chandler, p. 307, pl. 36, fig. 65.
1955 ?*Anemia colwellensis* Chandler, p. 304, pl. 35, figs. 39, 40, 42–53; pl. 36, figs. 59–64; text-fig. 2, 1.

In 1955 it was suggested that this Bembridge species might conceivably be barren material of *Anemia colwellensis*. There is a resemblance to the pinnule segments of this species both in the flabellate nervation and in the smoothness of the margins. Further experience of *Anemia* lends support to this view but as no conclusive evidence can be produced the barren pinules are merely referred doubtfully to the Colwell species.

GYMNOSPERMAE

Order CONIFERALES

Family ARAUCARINEAE

Genus ***ARAUCARITES*** Presl, 1838 : 203

Araucarites gurnardi Florin

1926 *Araucarites gurnardi* Florin *in* Reid & Chandler, p. 48, pl. 2, figs. 6–19.
1926 *Doliostrobus* sp. (*Araucarites gurnardi* ?) Reid & Chandler, p. 52, pl. 2, figs. 17, 18.
1961*a* *Araucarites gurnardi* Florin : Chandler, p. 27.
Araucarites gurnardi Florin : Chandler (in press), p. 39, pl. 1, fig. 3 ; pl. 2, figs. 4, 5.

A few additional facts are available about the cuticle of *Araucarites gurnardi* some of which have been mentioned by Chandler (1961*a* : 27). In contrast to *A. selseyensis* the stomatal bands extend almost throughout the length of the leaf on the dorsal side. On the ventral side there are more stomata in an uninterrupted line (sometimes as many as ten) in *A. gurnardi* than in *A. sternbergi* Goeppert (=*A. goepperti* (Sternberg) of Gardner) from the Bournemouth Beds (described Chandler, in press, pl. 1, figs. 1, 2, 4–13 ; pl. 2, figs. 1–3, 6–10 ; pl. 7, fig. 12). On the whole the ordinary epidermal cells tend to be more parallel-sided and rectangular-ended while pits (or papillae) are a most conspicuous feature. As in other species a double ring of subsidiary cells is commonly present around the stomata. The outer stomatal pore may be 0·02 to 0·03 mm. long, exceptionally up to 0·046 mm. It is usually elliptical but sometimes subcircular. For additional figures of *A. gurnardi* cuticle and remarks see Chandler (in press, pl. 1, fig. 3; pl. 2, figs. 4, 5). There are also eleven slides (V.44306–16).

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family POTAMOGETONACEAE

Genus ***POTAMOGETON*** Linnaeus

? *Potamogeton* sp.

(Pl. 33, figs. 148, 149)

Description. At least five layers of leaves preserved as impressions and arranged radially around a central axis or stem producing a superficial resemblance to a flower. In vertical thickness the specimen measures not more than 7 mm. The leaves are obovate, broadest at a little above the middle, flat, thin, probably sessile, with finely toothed margins (Pl. 34, fig. 149), the teeth being spaced at intervals of 1·25 to 1·5 mm. ; midrib prominent on the lower surface, broader and thicker than the subparallel lateral nerves (three or more pairs) which flank it on each side. The nerves converge both towards the base and apex and unite at the apex. The interspaces between these nerves are subdivided by thin, short, straight, longitudinal and transverse nerves into oblong spaces (0·15 by 0·1 mm. in diameter) accurately aligned in transverse rows. The oblong spaces are again subdivided by finer nervules into polygonal spaces, 0·6 by 0·3 mm. to 0·3 by 0·25 mm. in diameter ; these are filled by large hexagonal cells (0·05 mm. in diameter) which form the substance of the lamina. Certain small confused impressions near the stem suggest the presence of short broad stipules, but the leaf bases are so close together that it is not possible to be sure of this. The epidermis is smooth and formed of small longitudinally aligned cells (0·025 by 0·016 mm. in diameter). Usually it is not preserved and the surface then shows impressions of the large hexagonal cells within.

Remarks and Affinities. One specimen preserved in a waterworn nodule which when split along the bedding plane showed counterpart impressions. V.23428 shows the under surface of the leaves which evidently floated with blades expanded and have been embedded in this position. The internodes appear to have been very short, since the nodes lie accurately one above the other as indicated by the centres from which successive layers of leaves radiate. The leaves appear to have been arranged in whorls, but this may possibly be a secondary effect and they may actually have been alternate, separated only by short internodes and therefore appearing as a radiating series. V.23428*a*, which is figured, shows the upper surface. It is not easy in the fossil to distinguish between true nerves and the bast bundles which run the length of the leaves and provide supporting tissue in *Potamogeton*. Every character but one described above is found in the genus, the exception being the compacted arrangement of the leaves due apparently to the absence of petioles combined with the shortness of the internodes. The relationship is undoubtedly with Potamogetonaceae, and possibly with *Potamogeton* itself, fruits of which have been described from the Insect Limestone (Reid & Chandler, 1926 : 66, pl. 3, figs. 20–22). Two other kinds of leaves referred to *Potamogeton*, both distinct from those described above, occur at this horizon (Reid & Chandler, 1926 : 67, 68, pl. 3, figs. 23, 24 ; pl. 4, fig. 9). It must, however, be remembered, that fruits referable to two species of an extinct genus of Potamogetonaceae, *Limnocarpus*, were also described from the deposit. Fruits of *Limnocarpus* are intermediate between *Potamogeton* and *Ruppia* in characters. It is therefore possible that the leaves under discussion belong to *Limnocarpus*, so the generic determination must be regarded as doubtful. From the Insect Limestone, Thorness Bay.

Genus ***LIMNOCARPUS*** Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus forbesi (Heer)

(Pl. 33, figs. 150–153)

See p. 338.

V.43930–32 (figured) and V.43933 (numerous unfigured endocarps) were collected by C. Reid in the Bembridge Marls "below Chapel Corner, Wootton", a new locality for the species.

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes neglectus Chandler

(Pl. 34, figs. 154, 155)

See p. 359.

Reid & Strahan (1889 : 198) in describing the Bembridge Beds state that in the

Brickyard at Werror " the junction of the Hamstead and Bembridge Beds is apparently shown. Above a black seam were found *Melania turritissima*, *M. Forbesii*, *Melanopsis*, *Paludina lenta*, Fish bones, and *Folliculites thalictroides* [*Stratiotes neglectus* ?] with other seeds, but the strata are so weathered that it is not easy to obtain details of the section, and it is possible that this black seam may be somewhat higher than the Black Band " (the base of the Hamstead Series). See also p. 372. If the seeds labelled Werror are indeed from the Hamstead Beds then the range of *Stratiotes neglectus* is extended higher than was previously recorded.

Additional material: V.40079 holotype, figured Chandler, 1923, pl. 5, fig. 27 and Pl. 34, figs. 154, 155. V.40080 figured Chandler, 1923, pl. 5, fig. 4. V.43934 figured Chandler, 1923, pl. 5, fig. 28. V.16540, V.43935–37 seeds. All the above from the Bembridge Marls, Hamstead Ledge. V.40082 and V.43938 include numerous seeds from the Bembridge Marls, Thorness Bay. There are also seeds in various stages of decay from Brick pits or Bore-holes in Bembridge (or possibly Hamstead ?) Beds collected by J. Rhodes and found in J. Groves' Collections as follows: J.R.4358–59 seed Ashlake. J.R.3511 (49. 12ft.) seeds, J.R.4481 Bore-hole 201 13ft. J.R.4370 Rhodes No. 7A from Werror and J.R.4367 No. 7 from carbonaceous clay Werror (V.43939).

Family ARACEAE

Section MONASTEROIDEAE Engler

Genus ***RAPHIDOPHORA*** Hassk (or ***EPIPREMNUM*** Schott)

Epipremnum ? (or ***Raphidophora*** (***?***)) ***ornata*** Reid & Chandler

1926 *Epipremnum ornatum* Reid & Chandler, p. 83, pl. 4, figs. 24, 25.
1958 *Epipremnum ornatum* Reid & Chandler: Dorofeev, p. 173.
1958*a* *Epipremnum ornatum* Reid & Chandler: Dorofeev, p. 543.
1959 *Epipremnum ornatum* Reid & Chandler: Dorofeev, p. 1104.
1960 *Epipremnum ornatum* Reid & Chandler: Kolesnikova, p. 118, pl. 7, fig. 2.
1961 *Epipremnum ornatum* Reid & Chandler: Kolesnikova, pp. 126, 128, pl. 10, fig. 4.

This Bembridge species is also recorded from a number of deposits in the U.S.S.R., viz. Oligocene of Rezhenka (Dorofeev, 1958: 173), of Byeloyarna on the River Tavda (Dorofeev, 1958*a*: 543) and of Koziulino on the River Tom (Dorofeev, 1959: 1104) all in Western Siberia. It also occurs in Miocene localities (Kolesnikova, 1960: 118, pl. 7, fig. 2; 1961: 126, 128, pl. 10, fig. 4). The uniform spongy equiaxial cells throughout the testa in the species are not fully in accord with the structure of *Epipremnum* as shown by Kirchheimer (1957, pl. 12, fig. 54*a*) and it seems probable that these seeds should be referred to the related genus *Raphidophora* (Dorofeev ex. lit. 9.5.59). The reference to *Raphidophora* is provisional only pending detailed study of living material. The genus occurs in the East Indies, tropical and subtropical Himalayas, the mountains of Malaya and is common in China. *Epipremnum* has a similar range but penetrates further south to Australia, Tasmania and New Zealand.

Family ZINGIBERACEAE

Genus ***SPIREMATOSPERMUM*** Chandler, 1925 : 17

? Spirematospermum wetzleri (Heer)

(or ***S. headonense*** Chandler)

1925 *Spirematospermum wetzleri* (Heer) Chandler, p. 17, pl. 1, fig. 8*a–c* ; text-fig. 5.
1926 *Spirematospermum wetzleri* (Heer) : Reid & Chandler, p. 84, pl. 5, figs. 6, 7.
1961*b* ? *Spirematospermum headonense* Chandler, p. 108, pl. 24, figs. 28–30 ; pl. 25, figs. 31, 32.

In rediscussing material of *Spirematospermum* from the Lower Headon of Hordle now referred to a distinct species from *S. wetzleri* (Chandler, 1961*b* : 108) the writer pointed out that the small size of the isolated seeds obtained from the Bembridge Beds suggests that they should possibly be redesignated *S. headonense.* Evidence is, however, insufficient for certainty on this point. A tiny but characteristic spirally striate fragment of seed (J.R.3511 49. 12ft.) was found in the Ashlake Brickpit by J. Rhodes where the upper part of the Bembridge Marls is seen (Reid & Strahan, 1889 : 175) and it probably came from this horizon as it was associated with *S. neglectus*. However, it must be borne in mind that the Black Band and lowest beds of the Hamstead Series were also exposed in this pit and the collector Rhodes made no definite statement about the horizon.

Class DICOTYLEDONES

Family ULMACEAE

Genus ***CELTIS*** Tourn.

Celtis edwardsi n.sp.

(Pl. 34, figs. 156–160)

Diagnosis. Endocarp ovoid, reticulations of surface rather coarse and shallow as compared with many living species. Length about 3·5 mm. ; breadth in plane of symmetry, 3·5 mm. ; breadth at right angles to plane of symmetry, 3 mm.

Holotype. V.43919.

Description. *Endocarp :* One-loculed, one-seeded, ovoid but bisymmetric, pointed at the apex when perfect, with thick longitudinal ribs from which others diverge so as to form a coarse network in the meshes of which are shallow concave alveolae ; at the base (Pl. 34, fig. 159) four of the ribs, approximately at right angles to one another, are more conspicuous than the rest, two opposite ribs being continued to the apex where they become very prominent ; these lie in and emphasize the plane of symmetry. The other two may merge into the general network but may reach the apex. The apical prominence is pierced by a small median funicular canal leading to the apical placenta ; on each side of the prominence is a small median external depression delimited by a curved rib of the network (Pl. 34, figs. 156, 158). Surface cells irregularly polygonal 0·025 to 0·05 mm. in diameter. On the internal cast (=seed) is an apical rib corresponding in position with the external prominence, it is the cast of a depression in the locule in which the radicle lay. Average length of endocarp, 3·5 mm. ; breadth in plane of symmetry, 3·5 mm. ; breadth at right angles to plane of symmetry, 3 mm.

REMARKS AND AFFINITIES. Nineteen specimens. Some are endocarps (V.43919, V.43921–22) others external or internal calcite casts. They are preserved in white limestone labelled F. E. Edwards Collection, Headon Hill. Similar material from the F. E. Edwards Collection in the Sedgwick Museum, Cambridge, has the additional information that they were from the Bembridge Limestone, Headon Hill. In the British Museum (Natural History) collection no horizon is mentioned.

Form and structure indicate *Celtis*. In size and in the somewhat ill-defined ridges bounding the alveolae the closest resemblance is to *Celtis sinensis* (China) and *C. rubronervia* var. *integrifolia* (Phillipines), but the fossils are somewhat smaller than the former and larger than the latter species. They are also more ovoid, the above mentioned living fruits being subglobular. The fossil endocarps are much smaller than either *C. australis* or *C. occidentalis* and the net veining is relatively much coarser than in these species. The fossil records of *Celtis* endocarps are too numerous to quote. The genus is especially abundant in American deposits. The Isle of Wight species is exceptionally small. It has been named after the finder F. E. Edwards who collected the material in 1867.

Family NYMPHAEACEAE

Genus ***BRASENIA*** Schreber

Brasenia ovula (Brongniart)

See p. 346

The seeds are too familiar and common to need further description as regards their general characters, but the preservation of the Bembridge specimens from Ashlake now makes it possible to add a few details about the cell structure. The surface cells of the embryotega are large and oblong. The hard testa, columnar in section, 0·075 to 0·1 mm. thick, is formed of interlocking deeply digitate cells in which the digitations reach almost to the centre of the cells, they are few in number from about three to six, commonly three divisions being seen at the centre which branch or broaden towards their extremities. The diameter of the cells measured from the ends of the digitations is from 0·05 to 0·075 mm. The inner surface of this columnar coat presents a honeycombed appearance, the cells on this surface measuring 0·025 to 0·05 mm. in diameter and having irregularly thickened margins. Within there is a second coat which may be 0·05 mm. thick. It is formed of small cells, 0·012 mm. in diameter ; its outer surface is also honeycombed or pitted, the pits measuring 0·025 to 0·05 mm. This coat although in the closest contiguity with the testa is usually free from it in the fossils. It is sufficiently hard and resistant to preserve its form when the columnar coat has been removed. No doubt the honeycomb cells of the contiguous surfaces of the outer and inner coats are the outer and inner ends of the same layer of cells through which splitting has occurred in fossilization. The aperture of the embryotega pierces both coats. The tegmen which is tough and hyaline is formed of equiaxial cells (about 0·05 mm. in diameter) except around the embryotega where they are broader than long and arranged in concentric rows. Living

Brasenia seeds are always smaller than the largest fully developed fossils and their digitate cells appear larger and simpler with thicker digitations. However, there is a similar succession of coats, namely an outer columnar coat (0·2 mm. thick) with digitate cells (0·1 mm. in diameter) fused with an inner coat, somewhat spongy in texture (0·05 mm. thick) formed of small cells (0·01 to 0·0125 mm. in diameter). The tegmen is of equiaxial cells 0·0725 mm. in diameter.

Further material is from Ashlake Brickpit, Wootton Bridge, J. Rhodes Collection 4356 and 4357, also 4359 (labelled " 5A Ashlake ") and seed-casts labelled " 46 9·6″ to 11ft." There are seeds from Werror (? Bembridge Marls) J. Rhodes labelled " J.R. 4371 No. 7A Werror " and a few poorly preserved seeds from a Borehole " J. Rhodes 4436. BH 115. 14 to 15½ ft." V.32241 from the Upper Bembridge Marls, Whitecliff Bay, below Old School House.

Family RANUNCULACEAE

Genus ***RANUNCULUS*** Linnaeus

Ranunculus ovaliformis (Reid & Chandler)

(Pl. 34, fig. 161)

1926 *Samaravectis ovalis* Reid & Chandler, p. 142, pl. 9, figs. 14–16.

EMENDED DIAGNOSIS. Achene flattened obovate with broad, triangular, tapering style usually with reflexed tip. Seed-body small, central, achene bearing a few scattered tubercles which overlie it. Attachment giving rise to a narrow truncation. Margin of achene beyond limits of seed wing-like with radial striae.

ADDITIONAL MATERIAL. V.23429.

DESCRIPTION. *Achene :* One-seeded, subobovate, much flattened laterally, prolonged asymmetrically at the apex into a broad triangular tapering flattened style usually recurved at the tip which is finely pointed. The attachment slightly truncates the narrow end (Pl. 34, fig. 161). Seed only about one-third of the length and breadth of the achene, flattened obovate, represented by an internal cast in V.17628 (cf. Reid & Chandler, 1926, pl. 9, fig. 16 shown inverted). Surface of achene slightly inflated over the seed but flattened beyond so as to give the appearance of a wing-like flange beyond the locule. Funicle passing into fruit at the base where it forms a conspicuous ridge (channel on impression). Entry into seed not clearly seen but apparently at one side of its long lateral margin making the seed half anatropous. Surface of style longitudinally striate. Surface of fruit radially striate, the striae diverging from the margin of the seed, formed of elongate cells with sinuous outlines. On the central area which overlies the seed there are a few scattered small tubercles or processes (seen as pits on the impression). Surface of seed finely pitted. Length of V.23429,6 mm. ; breadth, 4 mm. Length of specimens previously described, 6 mm. ; breadth, 3·5 mm. Length of seed-cast, 2·5 mm. ; breadth, 1·5 mm.

REMARKS AND AFFINITIES. These impressions were not fully understood in 1926 and were therefore wrongly interpreted. They were then described and figured upside down. The difficulty of interpretation was enhanced by the poor preservation of the style (described as a stalk) in the holotype (V.17626) and in the figured specimen on V.17627. The style was also poorly preserved in V.18112, both it and the holotype lacking the flange-like margin which passes into the flanged region of the achene. Again in V.18111 the style appears to be obscured or broken. The discovery by G. W. Colenutt of a finely preserved specimen at Thorness Bay made the true affinities of the species clear. The majority of living species of *Ranunculus* differ in having a large seed surrounded by a narrow marginal longitudinally striate rib in place of a flange simulating a wing around a relatively small seed. *R. asiaticus* has a large flat recurved style, small seed-body and broad flange radially striate in the upper part of the achene much as in the fossil. Its size is similar but the seed-body is situated in the lower half of the fruit, not medianly, and the shortest margin between attachment and style is longitudinally striate. *R. nissianus* has a narrower flange around a relatively larger seed but has sparse tubercles scattered over the external surface overlying the seed as in the fossil. Such processes are larger and more conspicuous in *R. trilobus* and *R. parviflorus*. The species can now therefore be referred to *Ranunculus* as *R. ovaliformis*, the change of specific name being due to the preoccupation of *ovalis* within the genus *Ranunculus*.

INCERTAE SEDIS

Genus ***CARPOLITHUS*** Linnaeus

Carpolithus sp.

(Pl. 34, figs. 162–165)

1926 *Carpolithus* sp.2, Reid & Chandler, p. 143, pl. 9, fig. 18.
1926*a* Unidentified endocarp, Reid & Chandler, p. 378.

Description. *Fruit:* Obovate to broadly obovate in outline, having a thin brown epicarp separated from a thick hard endocarp by a layer of matrix impregnated with carbonaceous material (mesocarp ?). Length of fruit (imperfect), 11·8 mm.; breadth, 11 mm.

Endocarp: Bisymmetric, obovate in outline with small apical mucro, somewhat flattened near the margin in the lower third giving a flanged effect; dehiscing in the plane of symmetry into equal valves, smooth externally, woody, 0·7 mm. thick about the middle, close-textured formed of parenchymatous tissue; pierced at the base by a pair of canals which are continued as grooves inside the locule one on each side in the plane of symmetry. From the grooves and from the base coarse fibres arise branching and anastomozing to form a network over the surface of the locule. Seed not seen. Length of endocarp, 8 to 9·75 mm.; breadth, 7·75 to 8 mm. Thickness incomplete, less than breadth.

Remarks. Three specimens, possibly four, have been seen. V.17630 shows remains of fruit surrounding endocarp and was figured in 1926 (see reference above). Two specimens were later found by Mr. J. F. Jackson in a marly pocket in the Bembridge Limestone, Sticelett Ledge, near Gurnard. These are preserved in the Sandown Museum, Isle of Wight. A preliminary note recording the discovery was published by J. F. Jackson with a note on the plants by Reid & Chandler (1926*a*: 378), but there was no description nor was the connexion with *Carpolithus* sp.2 then recognized. One specimen represents a single valve and shows the outer surface and that of the locule. The second shows one valve virtually perfect with the upper part of the second valve still adherent, the lower part having been broken. The mode of dehiscence and smooth suture are clearly seen. Both are here illustrated for the first time.

(d) *The Hamstead Beds*

Horizons and localities as given in the text.

GYMNOSPERMAE

Order CONIFERALES

Family TAXODINEAE

Genus ***SEQUOIA*** Endlicher

Sequoia couttsiae Heer

See p. 336.

Material from the Hamstead Beds was listed and figured by Chandler (1962, pl. 1, fig. 23; pl. 3, figs. 11–13; pl. 4, figs. 1–4, 24–26, 28–32; text-fig. 2(1)). This material and V.42344–48 was obtained by G. W. Colenutt from blocks of cement-stone fallen from the cliff at Hamstead. Heer (1862) figured cones, twigs and seeds prior to the publication of his fuller account of better preserved material from Bovey Tracey, Devon, so that Hamstead is in fact the type locality for this species (Chandler, 1962 : 21). Most of Heer's material came from the Lower Hamstead Marls from a bed 7ft. above the " Black Band " of Forbes. Heer identified with his own species " *Taxites parisiensis* Brongn." recorded by Forbes (1886 : 47) from the "Hempstead Beds ". There are also slides 41045*a–d* prepared by Bandulska showing fragments of cuticle from Gardner's figured material 41045 (1883, pl. 6, fig. 2) see also 41423, V.15121–23. *Sequoia* twigs from 7ft. above the Black Band and specimens figured by Heer (1862, pl. 18, fig. 2) and by Gardner (1883, pl. 6, fig. 3) are in the Geological Survey Museum.

ANGIOSPERMAE

Class MONOCOTYLEDONES

Family TYPHACEAE

Genus ***TYPHA*** Linnaeus

Typha latissima Al. Braun

(Pl. 34, figs. 166–170)

1851 *Typha latissima* Al. Braun *in* Stizenberger, p. 75.
1926 *Typha latissima* Al. Braun : Reid & Chandler, p. 60, pl. 3, figs. 4–11.

Description. *Seed :* Pendulous, anatropous, elongate-ovoid, truncate at the micropyle, pointed at the chalaza which is indicated by a darkening and thickening of the testa. Micropyle large, closed by a flat disc with a central mucro ; raphe lateral, filiform. Testa formed of an outer light brown layer with hexagonal, transversely elongate cells, the angled ends of which alternate so as to produce zig-zag longitudinal ridges, these cells are about 0·05 mm. in transverse diameter and about 0·016 to 0·025 mm. in longitudinal diameter. One specimen shows a network of equiaxial cells with raised walls about 0·016 to 0·025 mm. in diameter. There is an inner delicate hyaline layer (tegmen ?) formed of long slender cells tapering at both ends. Dimensions of seeds: 1) Length, 1·1 mm.; breadth, 0·5 mm. 2) Length, 1 mm.; breadth, 0·4 mm. 3) Length, 1 mm.; breadth, 0·45 mm. 4) Length, 0·8 mm.; breadth, 0·35 mm. 5) Length, 0·95 mm.; breadth, 0·45 mm.

REMARKS. Numerous seeds, identical with those from the Bembridge Beds. The relationship to living species is fully discussed by Reid & Chandler (1926 : 60). In addition to the figured material there are eight seeds from the Waterlily Bed at Hamstead (V.43945) and five from the same horizon at Bouldnor (V.43946).

Family SPARGANIACEAE

Genus ***SPARGANIUM*** Linnaeus

? *Sparganium multiloculare* Reid & Chandler

(Pl. 34, fig. 171; Text-fig. 5)

1926 *Sparganium multiloculare* Reid & Chandler, p. 63, pl. 3, figs. 12–18.

See p. 340.

DESCRIPTION. *Endocarp*: Woody, truncate ovoid, four-loculed, conspicuously grooved and angled longitudinally, the grooves lying between the locules emphasized by abrasion so that the locule cavities are in part exposed (Text-fig. 5). Carpels distinct and obconical at the base, truncate and slightly concave at the apex which is pierced by the large stylar canals, one to each carpel. Locule cavity ovoid, lined by small transversely aligned cells. Length of endocarp, 2·5 mm.; breadth, 1·9 by 0·9 mm. Seed not seen.

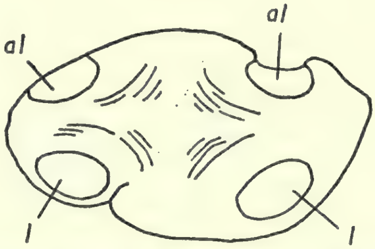

FIG. 5. ? *Sparganium multiloculare* Reid & Chandler. Diagrammatic drawing of the apex of endocarp showing apertures of four locules *l*, those marked *al* partly exposed on sides by abrasion.

REMARKS. One endocarp (V.43947) now collapsed. Although a small example, this endocarp agrees in other respects with *Sparganium multiloculare* from the Bembridge Beds, a species normally about 4 mm. long, to which therefore it is provisionally referred. From the White Band, Bouldnor.

Sparganium sp.

(Pl. 34, fig. 172)

Description. *Endocarp:* Woody, originally obovoid? but base incomplete, contours smooth, not conspicuously furrowed longitudinally, narrower at one side than at the other giving a suboval transverse section. Apex truncate pierced by a large circular stylar aperture leading into a solitary locule. Wall very thick, maximum thickness about 1 mm., texture close and compact, structure somewhat obscure but near the exterior formed of parenchyma with cells about 0·014 to 0·018 mm. in diameter. Locule lining concealed by decay. Length of endocarp incomplete (broken transversely just below the level of its maximum diameter). Diameter, 2·75 by 2 mm. Diameter of stylar aperture, 0·7 mm.

Remarks. The upper part of an endocarp, too imperfect for specific definition is undoubtedly a species of *Sparganium*. The solitary locule and smooth contours distinguish it from *S. multiloculare*. The single incomplete specimen (V.43948) is from the White Band, Bouldnor.

Family POTAMOGETONACEAE

Genus ***POTAMOGETON*** Linnaeus

Potamogeton tenuicarpus C. & E. M. Reid

(Pl. 34, figs. 173–176)

1910 *Potamogeton tenuicarpus* C. & E. M. Reid, p. 173, pl. 16, figs. 53, 54.
1957 *Potamogeton tenuicarpus* C. & E. M. Reid: Chandler, p. 85, pl. 11, figs. 12–14.

Description. *Fruit:* Broadly obovate, originally somewhat inflated but now much flattened, curved through almost a complete circle about a subcircular or oboval central depression, the curved area forming the locule; dorsal margin semicircular or gibbous, ventral margin slightly convex above and below, conspicuously indented between the ends of the limbs, i.e. between the convexities, at a distance of about a third of the length from the base of the fruit; sometimes there is a spine just above the indentation. Style small patent, terminal on the ventral margin. Surface having a conspicuous ridge around the central depression, around the dorsal margin adjoining the keel and along the middle of the keel, the ridges thin, forming sharp flanges. Keel broad reaching from the base almost to the apex, its median ridge flanked by a groove on each side. Surface cells about 0·012 by 0·02 mm. in diameter, somewhat irregular in shape aligned parallel with the curvature of the cavity, but also diverging from it. Length of endocarp, 1 to 1·5 mm.; breadth, 0·75 to 1·2 mm.

Seed: Narrow, elongate, curved like the locule; testa smooth shining, light brown, semitranslucent.

Remarks and Affinities. Numerous specimens. In size, form and in every detail of structure there is exact agreement with *Potamogeton tenuicarpus* C. & E. M. Reid from the Bovey Tracey Lignite to which species it is therefore referred. The width of the keel indicates that in life the degree of inflation may have been considerable. For comparison with *P. pygmaeus* see Chandler (1957 : 85). Szafer compares endocarps from the Miocene of Gliwice, Poland, with *P. tenuicarpus* (1961 : 84, pl. 23, figs. 19–21).

In addition to figured material from the Waterlily Bed of Hamstead (V.43949–50) and Bouldnor (V.43954–55) there are numerous unfigured endocarps from this horizon, V.43951 and V.43953 from Hamstead, V.43956 from Bouldnor and a few from the White Band, Hamstead (V.43952).

Genus ***LIMNOCARPUS*** C. Reid emend. Reid & Chandler, 1926 : 68

Limnocarpus forbesi (Heer)

(Pl. 33, fig. 153 ; Pl. 34, figs. 177, 178)

See p. 338.

Remarks. It seems unnecessary to repeat a description of this now familiar species but three figures for comparison with material at other horizons are given. Reasons for reverting to Heer's specific name have already been stated (Chandler, 1961*a* : 28, 29). In view of this discussion Hamstead must be regarded as the type locality for *Limnocarpus forbesi* even although most of the material from this locality and horizon is crushed and flattened and preserved on flat surfaces in which the carbonaceous remains are embedded. An exception to this rule is seen in the specimen in Pl. 34, fig. 177 collected by Colenutt at Hamstead cliffs, a fully inflated carbonaceous endocarp washed out of the matrix and now decayed. In addition to figured material from the Waterlily Beds of Hamstead (V.43960) and Bouldnor (V.43957) there are the following unfigured numerous crushed specimens: V.43958 (from Bouldnor), V.43961–64 from Hamstead, all from the Waterlily Beds, and V.43959 from the White Band of Bouldnor. All the above Groves Collection. Also 41040, labelled *Cyperites forbesi*, in grey marl, much crushed and others from Middle Freshwater Marls. 41039, H. Keeping Collection.

The early collectors invariably collected this species on slabs thickly beset with crushed endocarps (cf. Geological Survey Museum specimens referred to by Chandler, 1961*a* : 28) like the original holotype. A block with endocarps in the Sedgwick Museum, Cambridge is from the Middle Freshwater Beds Hamstead and is labelled *Cyperites ? forbesi* by E. A. N. Arber.

Family HYDROCHARITACEAE

Genus ***STRATIOTES*** Linnaeus

Stratiotes neglectus Chandler

(Pl. 34, figs. 181, 182)

See p. 359.

Some peculiarly well preserved and characteristic seeds were found at Hamstead by A. G. Davis in association with *Potamaclis turritissima*. They were labelled Hamstead Beds. Prior to this *Stratiotes neglectus* had been found only in the underlying Bembridge Beds, with some doubtful immature seeds in the Osborne Beds (see pp. 359, 363). If the horizon is indeed Hamstead the range of *S. neglectus* is extended upwards, but it should be noted that although the species *Potamaclis* (*Melania*) *turritissima* is listed by Reid & Strahan (1889 : 292) from both the Bembridge and

Hamstead Series it is recorded abundantly from the Bembridge Marls only, with the possible exception of beds they described on p. 198. Hence the horizon may be doubtful in a section where Bembridge and Hamstead Beds are both exposed having regard to the fact that in the seam, gastropods and *Stratiotes* both abounded. There is no need to repeat the description of the species already given by Chandler in 1923 and Reid & Chandler in 1926. Typical seeds from the Bembridge Marls are shown in Pl. 34, figs. 154, 155. Figured specimens labelled Hamstead Beds are V.43968–69 and unfigured material V.43970.

Stratiotes websteri (Brongniart)

(Pl. 35, figs. 183–186)

1923 *Stratiotes websteri* (Brongniart): Chandler, p. 128, pl. 5, figs. 7–12, 31; pl. 6, figs. 1–5, 26. See also for earlier references.

1957 *Stratiotes websteri* (Brongniart): Chandler, p. 86, pl. 11, figs. 15–19.

REMARKS. The species has been fully described in the above references and there remain only a few minor alterations or additions: viz. the longitudinal ridges which ornament the surface are rounded and interrupted; occasionally traces of ridges or tubercles are seen on the collar; the pitting on body, collar and keel is more or less uniform, typical pits measuring about 0·05 mm. in diameter. Length of seed varies from 5·25 to 7·5 mm.; breadth from 2·25 to 3 mm. A small probably abortive seed measured only 3·1 mm. in length; 2 mm. in breadth.

The seeds are very abundant at certain horizons and include among normally developed specimens a few which are exceptionally small. They are no doubt undeveloped and abortive specimens such as occur in the many-seeded fruits of living *Stratiotes*. A few of the large seeds show a thin adherent layer of clay with filmy light brown tissue embedded within it. This tissue arises from the woody testa and may be an outer dried up mucilaginous coat not commonly preserved in fossilization. The presence of these filmy remains suggests that the rounding of the longitudinal ridges and the shortness of the transverse raphe canal in the hard testa are not due to abrasion but are original characters in this species.

Many seeds from Hamstead have been compared with seeds from Bovey Tracey and from the *Cyrena*-marls of Offenbach on Main. Specimens from the three localities are indistinguishable although the Offenbach seeds tend to be somewhat smaller and rougher with a slightly smaller collar.

No holotype has ever been designated so V.43971 (Pl. 35, fig. 183) has been chosen. It was collected in the White Band at Hamstead and is a very typical well developed seed. In addition to figured material which includes V.43976 (Chandler, 1923, pl. 5, figs. 7–9), V.40070 (Chandler, 1923, pl. 5, fig. 31) and V.42039 (Chandler, 1923, pl. 6, fig. 1) there are the following: numerous seeds from the White Band V.16543, V.40072–73, V.43972 Hamstead, and V.43973, V.43977 Bouldnor and two from the Waterlily Bed (V.43978 Bouldnor). 14235 includes impressions of seeds ? *S. websteri* alleged to come from the Eocene of the Isle of Wight, presented by the Marchioness of Hastings, probably from the Hamstead Beds and V.40071, V.42040 from the Hamstead Beds

Allusions to *Stratiotes*, under the names *Carpolithes thalictroides*, *Carpolithes websteri* and *Folliculites thalictroides* are found in the Geological Survey Memoirs (Forbes, 1856 ; Bristow, 1862 ; Reid & Strahan, 1887) in accounts of the Hamstead Beds. As they are without figures or descriptions it is not possible to tell to which species (*S. websteri* or *S. acuticostatus*) the seeds in question really belonged. References to these names are given in detail in the synonymy by Chandler (1923).

Stratiotes acuticostatus Chandler

(Pl. 35, figs. 187–192)

1923 *Stratiotes acuticostatus* Chandler, p. 127, pl. 5, figs. 5, 6, 29, 30 ; pl. 6, fig. 25.

(Possible earlier allusions to the species (all doubtful) under the names *Folliculites thalictroides*, *F. websteri* or *Carpolithes websteri* are listed among the synonyms published by Chandler (1923). See note under *Stratiotes websteri* above.)

DIAGNOSIS. Seed oblong, oval or narrow-oval, often much flattened, very slightly hooked at the base ; keel usually broad, collar small, testa with conspicuous sharp serrated ridges, pitting coarse, pits up to 0·1 mm. in diameter, micropyle sub-basal, oblique ; hilum dorsal near the base, raphe marginal to the middle of the dorsal side, thence diagonal, diagonal portion normally less concave to the interior than in *S. neglectus* ; cells of the interior of the keel straight with their length parallel to the length of the keel. Length about 5·5 to 6·75 mm.

HOLOTYPE. V.40075.

REMARKS. The species was first described by Chandler in 1923. There is little to add to this account except that the surface pits of mature seeds are much coarser than those of *S. websteri* and *S. neglectus* and are commonly 0·1 mm. in diameter on the general surface and may be even larger on the keel. The length varies from about 5·5 to 6·75 mm. ; the breadth from 2·5 to 3 mm. Abortive small and ill developed specimens are however common(Pl. 35, figs. 190–192) and are sometimes segregated in separate pockets. A typical immature seed measures 4·25 mm. in length and 1·75 mm. in breadth.

In addition to the holotype (figured Pl. 35, fig. 187 and Chandler, 1923, pl. 5, fig. 5) and other figured material (V.44653 Pl. 35, fig. 189 and Chandler, 1923, pl. 5, fig. 6 ; V.40074 Pl. 35, fig. 188 and Chandler, 1923, pl. 5, fig. 30 ; V.44654 Chandler, 1923, pl. 5, fig. 29 now partly broken ; small seeds V.44174, V.44176, V.44179, Pl. 35, figs. 190–192) there are V.16541–42, V.44175, V.44180–83 comprising numerous seeds varying in degree of abrasion, all from Bouldnor Cliff and V.44184 from Hamstead. V.44177 are from the White Band, Bouldnor and V.44178 from the Waterlily Bed, Bouldnor. *Stratiotes websteri* and *S. acuticostatus* occur intermingled in the White Band, Hamstead Beds. 52613 is an indurated shaly slab of ironstone, not localized, but almost certainly Hamstead Beds. V.841 with an admixture of *Brasenia* : the *Stratiotes* sp indeterminable ? but may be a mixture of *S. websteri* and *S. acuticostatus*. V.44651 ? *S. acuticostatus* "Hempstead Beds". 52614 ? *S. acuticostatus* labelled Colwell Bay but is almost certainly from Hamstead.

Family CYPERACEAE

Section CARICOIDEAE

Genus **CARICOIDEA** Chandler, 1957 : 86

? Caricoidea minima (Chandler)

(Pl. 34, figs. 179, 180)

1961*b* *Caricoidea minima* (Chandler) : Chandler, p. 105, pl. 24, figs. 18–21.

See p. 340.

DESCRIPTION. *Endocarp :* Oburceolate, broadest at about the middle, pointed above, truncate below where it is narrowed into a short neck with spreading margin, pierced by a basal aperture. Length of neck more than one-sixth the length of the whole endocarp, width in the narrowest part about half that of the endocarp. Some specimens show two longitudinal ridges from base to apex, in others they are seen only on the neck dying out above. Sometimes they are absent altogether (abrasion ?). A tendency for the neck to be bilobed is noted, the lobes being continued into that part of the endocarp between the ridges when these are present, the concavities between the lobes marking the termination of the ridges. Surface rough, cells equiaxial, about 0·012 mm. in diameter, arranged in longitudinal rows especially on the neck so as to give an obscurely striate appearance. Walls thick, formed of parenchyma. Length of endocarp, 1·25 to 1·5 mm. ; diameter, 0·9 to 1·2 mm.

Seed : Represented by thin testa formed of transversely elongate cells which produce transverse striations.

REMARKS. Thirteen specimens, all but one much compressed, They are referred to the form-genus *Caricoidea* and provisionally to the species *C. minima* (Chandler). It is doubtful whether the spreading split neck is itself a specific character which could separate the Hamstead material from this Lower Headon species in view of the fact that varying degrees of spreading may be observed among living specimens of *Cladium mariscus.* A greatly exaggerated degree of spreading is apparent in *Caricoidea* (? *Cladium*) *colwellensis* from the Upper Headon (p. 340). The fruit characters seen in material from the Lower Headon of Hordle appear to separate these fossils definitely from the living *Cladium* (Chandler, 1961*b* : 106).

In addition to two figured specimens there are extant V.43967 from the Waterlily Beds of Bouldnor cliff and V.44842 from Hamstead Beds, Hamstead cliff.

Family PALMAE

Genus **SABAL** Adanson

Sabal major (Unger)

(Pl. 35, fig. 193)

1847 *Flabellaria major* Unger, p. 42, pl. 14, fig. 2.
1855 *Sabal major* (Unger) Heer, p. 88, pl. 35 ; pl. 36, figs. 1, 2.
1862 *Sabal major* (Unger) : Heer, pp. 373, 376.

Several leaves were found by Pengelley 7ft. above the Black Band which was taken by Forbes as the base of the Hamstead Series. They were described, but not figured, by Heer. Two he referred undoubtedly to *Sabal major,* they showed the end of a petiole and base of a leaf with long tapering rachis having a maximum breadth of 44 mm., with pinnules attached on both sides agreeing wholly in their insertion, form and nervation with *S. major*, so he stated. A third specimen was doubtfully determined. It represented the central part of a leaf with pinnules 10 to 12 mm. broad, each with a median ridge and with numerous longitudinal nerves between each pair of which were four finer nerves.

These specimens have not yet been traced but one of them may be in the Geological Survey Museum (XXI 2/3).

Another specimen was collected by Henry Keeping in 1888 from the Middle Hamstead of Hamstead (Pl. 35, fig. 193). It is still in the Sedgwick Museum, Cambridge. It shows the impression of the lower surface with long tapering rachis extending throughout the length of the fragment. The base of the blade is markedly asymmetric, there are about thirty pinnules but their distal ends are not preserved so it is not clear whether they are multifid or multiplicate away from the centre. There is no evidence about the stalk nor about the ligule. Remains only of the carbonaceous substance of the leaf can be seen, most of it having flaked away as the specimen dried taking with it the remains of the ligule. The length of the fragment along the rachis is 105 mm. and the breadth at right angles to this about the same.

It appears to be a species of *Sabal* and is comparable with the Bembridge specimens described by Gardner 76582 (1888 : 423, pl. 5, fig. 2) and Reid & Chandler V.17560 (1926 : 79, pl. 4, fig. 26) as *Sabal major*. V.42038 is an imperfect leaf showing the rachis.

DICOTYLEDONES

Family NYMPHAEACEAE

Genus ***BRASENIA*** Schreber

Brasenia ovula (Brongniart)

(Pl. 35, fig. 194)

See p. 346.

Seeds are as common in the Hamstead Beds as in the Lower and Upper Headon and Bembridge. All the typical characteristics of the species are shown. One seed (V.44185) is figured from Hamstead. In addition there are specimens from the White Band (V.44186) and Waterlily Bed (V.44188–89) Bouldnor ; from the White Band (V.2881), Waterlily Bed (V.44190), " Middle Freshwater Marls " (41422) and unspecified horizons (40902 internal casts only, 41041–42, 41044, V.44191) at Hamstead (=Hempstead). Some of the older material is labelled "Nymphaea Doris". V.841 from Hamstead is associated with *Stratiotes*, possibly *S. acuticostatus*.

Genus ***NELUMBIUM*** Juss.

Nelumbium buchi Ettingshausen

See p. 360.

Rhizomes and leaves attributed by Heer to *Nelumbium* occur, the former in abundance, especially in the strata which succeed the basal " Black Band ". They are found chiefly 7 ft. above this horizon. Usually the leaves are immature or represented by imperfect fragments only, but one all but perfect leaf (52712) was figured by Gardner (1888, pl. 4). According to the old label it was collected by H. Keeping in the Middle Freshwater Marls. Its actual margin was preserved in many places and the leaf was described in the following terms : " peltate, nearly circular in outline, notched on the uppermost margin and with radiating venation, the vein proceeding to the base of the notch being stronger than the rest. The principal veins fork, but reunite near the margin, and the secondary venation is obscure. The articulation with the petiole is very visible at the centre of the leaf ". At an earlier date, however, Heer (1862 : 374) had stated that delicate veins united the principal veins, the areas between them being filled up with fine reticulations [as in living *Nelumbium*].

The rhizomes, Heer states, are from 10 to 14 mm. thick but at the nodes, which may be 3 ft. apart, as much as 23 or 24 mm. thick. From the nodes numerous roots arise which fall away leaving crowded circular scars. Heer did not doubt the relationship of these rhizomes to *Nelumbium*, but Gardner (1888 : 417) pointed out that they appear to have been quite hollow, not fleshy and succulent as in *Nelumbium*. While accepting the leaves unhesitatingly as *Nelumbium*, he appears to have doubted the relationship of the rhizomes. Their hollow condition may however have been due to decay of pithy tissue in fossilization.

The rhizomes were associated with macerated fragments of sword-shaped leaves (*Sparganium* ? *Typha* ?) ; hence it is clear that more than one genus was represented in the bed. Possibly therefore more than two genera were present so that if Gardner's doubt was justified the rhizomes may have belonged to another plant.

Gardner (1888) in his description of plate 4 comments that the rhizomes were identified by Heer and by Saporta as those of *Nelumbium* but " hitherto no trace, either of the remarkable fruit, or of the seeds, has accompanied them ".

The striking abundance of Nymphaeaceae seeds, now referred to *Brasenia ovula* has been commented upon by older workers as well as by collectors at the present day. It is a peculiar phenomenon that abundant seeds of the family occur in certain beds of the Hamstead Series and rhizomes with leaves and abundant leaf fragments in another bed. It inevitably raises the question whether the supposed *Brasenia* seeds and *Nelumbium* leaves and rhizomes belong to the same plant and if they do should they really be referred to one of these genera or to some extinct genus. The answer to this query cannot at present be provided. Apart from Gardner's figured leaf there are the following rhizomes in the British Museum (Natural History) : 41043, 41421, 41425, V.1844–46, V.44828–30 labelled Middle Freshwater Marls.

Family ROSACEAE

Genus ***RUBUS*** Linnaeus

Rubus sp.

A single small, curved, laterally compressed spine with elongate base and smooth finely longitudinally striate surface, the striae being formed by small oblong longitudinally aligned cells. Length of spine, 2 mm. Similar spines were found at Hordle and Bovey Tracey both of which localities yielded *Rubus* endocarps. The spine has been compared with those of *Rubus* and *Rosa*, it agrees in cell structure with *Rubus*.

Family LEGUMINOSAE

Genus ?

(Pl. 35, fig. 195)

Description. *Seed:* Subglobular originally (now compressed). Hilum not seen owing to the compression. Surface smooth, cells small equiaxial producing a fine granulation, testa columnar in section, the ends of the columns producing the surface cells, breadth of columns about 0·006 mm., thickness of testa varying from 0·05 to 0·1 mm. Diameter of compressed seed, 3·3 by 2·5 mm. Two other specimens (decayed) possibly referable to the same species measured 3·2 by 3 mm. and 2·7 by 2·6 mm. respectively.

Remarks and Affinities. These seeds at first sight resemble *Brasenia*, but no embryotega could be seen nor any digitate cells. When fractured to show the testa in section, the radial columns appear to be much narrower and longer than in *Brasenia*. The difficulty of detecting a hilar scar along the flattened edge suggests that this organ was very small, probably situated at the split in the margin. The relationship seems to be with Leguminosae, but there is insufficient evidence on which to base generic determination. V.44192 from the Hamstead Beds of Hamstead.

Family DROSERACEAE

Genus ***ALDROVANDA*** (Monti) L.

Aldrovanda intermedia Reid & Chandler

(Pl. 35, fig. 196)

1926 *Aldrovanda intermedia* Reid & Chandler, p. 113, pl. 6, figs. 27–29.

Description. *Seed:* Oburceolate, with a narrow neck about one-seventh the length of the seed; anatropous with longitudinal raphe ridge terminating in an apical mucro. Surface glistening, flatly tubercled, the tubercles about 0·025 mm. in diameter and less convex than those of *Aldrovanda ovata*. Inner coat not seen. Length of seed, 1·65 mm.; diameter, 1·2 mm.; length of neck, 0·2 mm.

Remarks. One seed (V.44193) slightly broken at the neck. It agrees in size and shape and in the character of the tubercles with *Aldrovanda intermedia* Reid & Chandler from the Bembridge Beds. It is smaller than *A. ovata* from the Lower Headon of Hordle and Lower and Upper Headon of Colwell Bay.

Family AQUIFOLIACEAE

Genus ***ILEX*** (Tourn.) L.

? Ilex sp.

(Pl. 35, fig. 197)

Description. *Endocarp:* Rounded-oblong in outline, inflated, rounded triangular in section, with a median ventral angle, the angle being formed by a thick fibro-vascular strand which gives off two alternating branches one on each side. The vascular strand passes from a large oval basiventral scar of attachment to the apex of the ventral ridge where it makes a slight prominence. The carpel wall adjacent to this fibre strand is formed externally of coarse parenchyma beneath which the cells are aligned transversely. The dorsal surface is covered by a closely adherent layer of longitudinally striate fibres, the striations being parallel, not converging at the two ends, slightly oblique. It is not clear whether this layer forms part of the carpel wall or is accidentally adherent to it. Length of endocarp, 3 mm. ; breadth, 1 mm. (increased by compression).

REMARKS. One endocarp (V.44194) from Hamstead represented by an internal cast in coarse-grained pyrites to which the carpel wall adheres on the ventral side. Size and form, position and character of attachment, the ventral vascular strand and its mode of branching, are identical with the characters seen in certain species of *Ilex* but there is nothing in the living carpels to correspond with the longitudinally striate dorsal layer described above. In *Ilex* all the inner horny layers are formed of transverse fibres with an admixture of oblique fibres. If, however, as suggested by the strict parallelism of these fibres with no hint of convergence to the attachment scar the longitudinal layer is not organically connected with the endocarp, but is only accidentally adherent to the specimen, then the structure indicates relationship with *Ilex*.

Family ?

Genus ***RHAMNOSPERMUM*** Chandler, 1925 : 30

Rhamnospermum bilobatum Chandler

See p. 355.

Additional material has been found in the Hamstead Beds where some seams are crowded with this plant which is often associated with *Stratiotes acuticostatus*. V.40937 (figured Chandler, 1962, pl. 24, fig. 5) from Hamstead. V.40938 (figured Chandler, 1962, pl. 24, fig. 6), V.44195–96 from Bouldnor cliff. V.44197–99 from the Waterlily Beds, Bouldnor.

INCERTAE SEDIS

Genus ***CARPOLITHUS*** Linnaeus

Carpolithus sp. (***? Spirematospermum*** sp.)

(Pl. 35, fig. 198)

DESCRIPTION. *Pod :* Lanceolate, curved, incomplete at one end (apex ?), tapering to the other where there is a rounded point which appears to have been abraded. Angled longitudinally (original ?) above and below with about four strong longitudinal ribs on the exposed surface, narrowly ellipsoid in transverse section. Number of locules almost certainly one. Surface formed of hexagonal cells arranged in regular longitudinal rows, cells about 0·038 to 0·057 mm. parallel with the length of the pod, 0·057 mm. at right angles to it. Wall about 0·5 mm. thick. Seeds not seen. Length preserved, 70 mm. ; maximum breadth, 9 mm. ; thickness, 3 mm.

REMARKS. The specimen lies with one surface embedded in matrix. It is not certain which end of the pod is broken but it seems probable that it is the apex which is missing. The surface cells very closely resemble those of *Spirematospermum headonense* from the Lower Headon of Hordle (Chandler, 1961*b* : 108, pl. 24, figs. 28–30 ; pl. 25, figs. 31, 32). It is possible that this pod belongs to the genus *Spirematospermum* but the evidence to establish this relationship is missing. In any case a different species is indicated as the Hamstead pod is much longer and narrower. Its original length cannot be estimated as, if it belongs to *Spirematospermum*, the apex would probably have terminated in a wide perianth disc without any appreciable narrowing of the pod towards it. One carbonaceous specimen (41424) from the Lower Hempstead Marls, Hempstead.

Carpolithus sp.

1888 *Gardenia? Wetzleri* Gardner, p. 417, pl, 3, figs. 11–15.

A fruit figured by Gardner and described as a rounded or subangular capsule with thick valves and two or more cells is ligneous, leathery and indehiscent. It had two rows of black and shining, angular, closely fitting seeds. Gardner records that on removing some of these a second layer of seeds was disclosed beneath a thin wall, hence his statement that the fruit was two-celled with four rows of seeds. Plate 3, fig. 11 (Gardner, 1888) shows the pod. Beside it but separate from it lies a thick stalk which does not appear to belong. Figs. 12–15 show the seeds natural size but there is no hint of the spiral striae seen in *Spirematospermum* (formerly *Gardenia*) ***wetzleri*** as represented on seeds from Bovey Tracey or the German lignite, on those of *Spirematospermum headonense* from the Lower Headon of Hordle or on detached seeds from the Bembridge Beds. As this characteristic feature is not mentioned either it does not seem probable that the pod (no longer extant) can have belonged to *Spirematospermum*. Indeed Gardner (1888 : 418) states " I am more inclined to place it under the Iridaceae ".

Carpolithus sp.

(Pl. 35, fig. 199)

DESCRIPTION. *Seed :* Obovoid, now much compressed, truncated by a gaping aperture at the narrow end. Testa formed superficially of pits or concave cells with sinuous outlines 0·025 to 0·05 mm. in diameter. Length of seed, 2·4 mm. ; breadth, 2·05 mm. One seed (V.44187) from the White Band, Hamstead. It has not been determined but may conceivably be a peculiarly preserved *Brasenia* in which case the aperture is that of the embryotega. As the form is not typical of a ***Brasenia*** seed the specimen has been referred to *Carpolithus* sp.

Carpolithus sp.

(Pl. 35, fig. 200)

A small flattened ovate seed or carpel, slightly asymmetric, with rough coat; attachment or chalazal scar at the middle of the broad end. Length, 2·1 mm., breadth, 1·5 mm. The systematic position has not been discovered. V.44200 from Hamstead Beds of Hamstead cliff.

Carpolithus sp.

(Pl. 35, figs. 201–204)

Small ovoid semitranslucent integuments (flattened in fossilization) with a projecting short cylindrical black organ at one end, often splitting median longitudinally at the other end. Cell structure obscure, but two coats can be distinguished, an outer (structureless ?) layer broadest near the chalaza, which forms a narrow marginal flange and an inner somewhat denser yellow coat. Dimensions of three typical specimens are as follows: 1) Length, 0·95 mm.; breadth, 0·52 mm. 2) Length, 1·1 mm.; breadth, 0·55 mm. 3) Length, 1·3 mm.; breadth, 0·6 mm.

These integuments suggest a tegmen with a large thick black chalaza. If this is a correct interpretation the testa must have decayed and vanished completely. It must, however, be borne in mind that the absence of any cell structure may indicate a chitinous substance. If so, they may perhaps represent egg cases, possibly of an insect, not a seed at all. At present their true relationship is quite obscure. They are abundant in the Hamstead Beds. In addition to figured material from the Waterlily Bed, Hamstead, there are V.44204 from the same horizon and locality and V.44205 from Bouldnor.

(e) *Horizon* ?

Locality Headon Hill.

Family ICACINACEAE

Genus ***STIZOCARYA*** Reid & Chandler, 1933 : 336

Stizocarya sp.

(Pl. 35, figs. 205, 206)

Description. *Endocarp :* Globular with a slight bisymmetry about a plane in which the funicle lies. Dehiscence into equal valves along this plane. External surface much abraded, smooth (secondarily ?) with numerous inconspicuous small pits marking the outer ends of cylindrical canals. These traverse the thickness of the wall at right angles to its surface and form similar but more conspicuous pits on the interior about 0·3 to 0·4 mm. apart. Canals occupied by compact oblong cells or fibres which form hair bases. Wall woody, 0·75 to 0·1 mm. thick, compact, formed of small parenchymatous cells, 0·016 mm. in diameter. Funicle only preserved near the apex where it traverses the wall diagonally to the apical placenta (Pl. 35, fig. 206). Length of endocarp, 15 mm.; breadth, 14 mm.

Remarks. Two endocarps, both broken so that the internal characters are displayed. They were in a box containing two differently preserved specimens obviously from other horizons. On the box lid was " F. E. Edwards Coll." and the late W. N. Edwards stated that it was in a batch of material which was sent to the British Museum (Natural History) as " Searles V. Wood Collection ". Inside the box was a label in F. E. Edwards' hand " Headon Hill ". The preservation and colour of these carbonaceous endocarps strongly suggest that they were derived from an ironstone nodule.

The form of the endocarp, mode of dehiscence and position of the funicle indicate the family Icacinaceae. The cylindrical canals which pierce the wall place the specimens in *Stizocarya* Reid & Chandler, a genus based originally on London Clay material. The endocarps agree closely in size and shape with *S. communis*, but in that species the canals are about 0·6 to 1 mm. apart and not therefore so close as in the species here described.

In view of the uncertainty as to the origin of the specimens no specific name has been given. Nevertheless they are of interest and importance as they indicate the presence of Icacinaceae in the Tertiary of the Isle of Wight and are certainly from a younger horizon than the London Clay. The probable occurrence in ironstone nodules suggests the Headon Beds. It is much to be hoped that further material will be found which will elucidate the origin of these endocarps. In addition to V.43928 which is figured, there is an endocarp V.43929.

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EXPLANATION OF PLATES

FIGS. 1–141 all from the cliffs of Colwell Bay, Isle of Wight, except figs. 16–19, 64, 65, 67–69 from the Lower Headon of Hordle, Hampshire (for comparison). Unless otherwise stated Colwell specimens are from Upper Headon Beds between Brambles and Linstone Chines.

PLATE 27

? *Araucarites gurnardi* Florin

FIGS. 1, 2. Distal end of cone-scale, base broken; short rounded apical process may be abraded. Fig. 1 dorsal surface, escutcheon above, *e*. Fig. 2 ventral. ×6·5. (V.43780.) Below sewer pipe, Linstone Chine.

Sequoia couttsiae Heer

FIG. 3. Twig tip with remains of male cone showing anthers. ×36. (V.44841.)
FIG. 4. Part of same at *x* in fig. 3. × 161. Between Colwell and Brambles Chines.

Pinus sp.

FIG. 5. Seed, upper surface showing cell structure; *m*, micropyle; *c*, cells of testa seen in section in edge of broken valve fragment. × 20. (V.43785.)

Potamogeton pygmaeus Chandler

FIGS. 6, 7. Endocarps with spines, keel, *k*, gaping; *p*, spiny process on ventral margin; *s*, style. ×18·75. (V.43787–88.) Below sewer pipe, Linstone Chine.

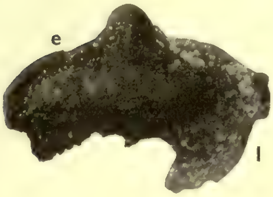
FIG. 8. Abraded endocarp with almost smooth contours crushed so that median gap between limbs appears small. × 18·75. (V.43793.)

Limnocarpus forbesi (Heer)

FIGS. 9, 10. Two endocarps in pyrites; *s*, style; *k*, keel. × 14. (V.43794–95.)

Stratiotes headonensis Chandler

FIGS. 11–19. Seeds. Fig. 15 small abortive specimen (V.43803). All others represented by one valve only. Figs. 11, 13, 14, 16, 19 show external surface. Figs. 12, 17, 18 internal surface with raphe canal, marginal in lower part, diagonal to apical chalaza above. Exceptional width of keel well shown in figs. 12, 18, 19. Figs. 16, 17 outer and inner surfaces respectively of a single seed and figs. 18, 19 of another. Figs. 11–15 × 6·5. Figs. 16–19 × 8. Figs. 11, 12 between Brambles and Linstone Chines. (V.43799–V.43800.) Figs. 13–15 below sewer pipe, Linstone Chine. (V.43801–03.) Figs. 16–19 for comparison from Lower Headon of Hordle. (V.42073, V.42078.)



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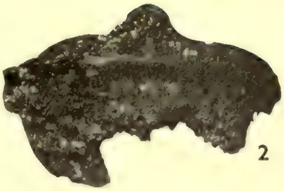

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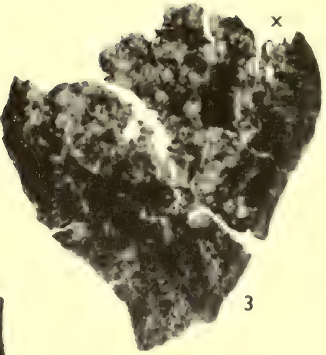

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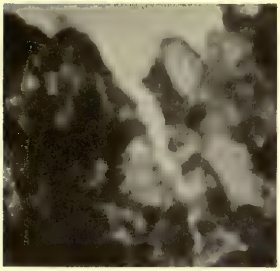

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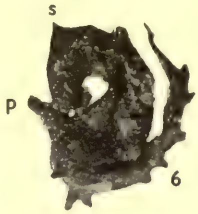

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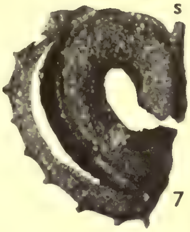

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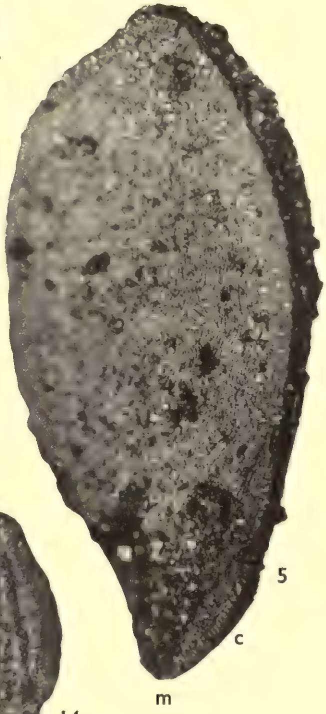

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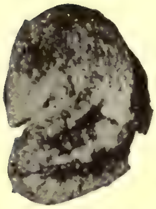

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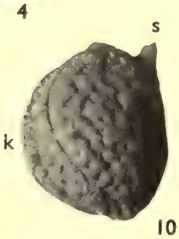

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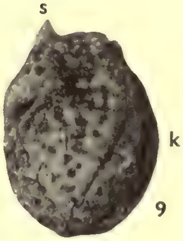

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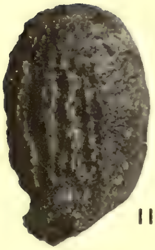

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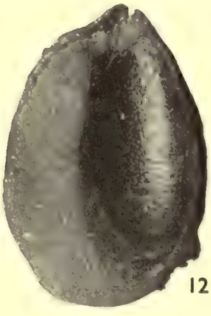

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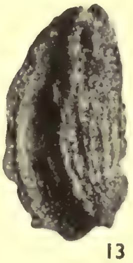

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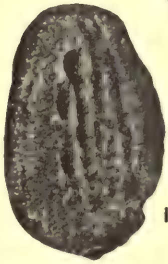

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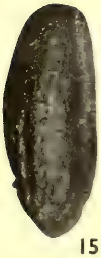

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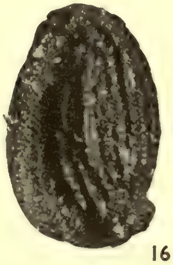

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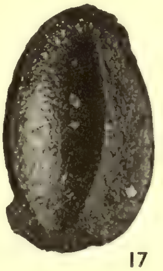

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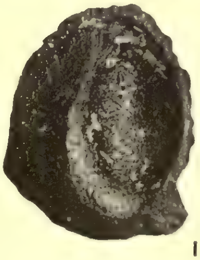

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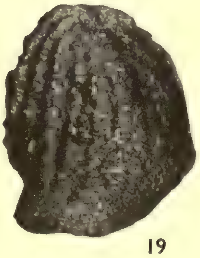

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PLATE 28

Carex sp.

Figs. 20, 21. Endocarp, opposite surfaces. Fig. 20 is the facetted side. × 20. (Decayed.)

Figs. 22, 23. Another, slightly broken at base. Facetted surface in fig. 23. × 20. (Decayed.)

Figs. 24, 25. Endocarp, slightly imperfect at apex. Facetted surface in fig. 25. × 20. (V.43807.)

Carex colwellensis n.sp.

Figs. 26, 27. Holotype. Endocarp, *s*, styles. × 20. (V.43808.)

? *Scirpus* sp.

Fig. 28. Fruit with longitudinal ridges. × 20. (V.43809.)

? *Caricoidea obscura* Chandler

Figs. 29, 30. Two endocarps. × 15. (V.43824, V.43826.)

Caricoidea (? *Cladium*) *colwellensis* n. sp.

Fig. 31. Broad endocarp. × 14. (V.43812.)
Fig. 32. Holotype. Endocarp. × 14. (V.43810.)
Fig. 33. Small endocarp. × 14. (V.43811.)
Fig. 34. Endocarp showing longitudinal ridge. × 14. (Decayed.)
Fig. 35. Endocarp tilted to show basal aperture. × 14. (Decayed.)

Caricoidea maxima Chandler

Fig. 36. Fruit, side. × 14. (V.43815.)

Fig. 37. Another fractured longitudinally but irregularly so that upper half of endocarp, *e*, is exposed in longitudinal section. Its lower end lay about one-quarter of the length of the fruit from its base. Some coarse polygonal cells preserved in pyrites seen near the base of the cavity may be adherent foreign tissue. × 14. (Decayed.)

Fig. 38. Another fruit abraded at base so that endocarp is exposed showing basal aperture. × 14. (Decayed.)

Fig. 39. Endocarp released from fruit tilted to show apex, so that neck, *n*, almost hidden. × 14. (V.43816.)

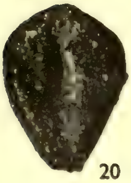
Fig. 40. Another endocarp with conspicuous neck but no apical mucro. Tilted to show apex. × 9. (V.43817.)

? *Caricoidea angulata* Chandler

Figs. 41, 42. Two endocarps. × 14. (V.43818–19.)

Cyperaceae. Genus ?

Figs. 43, 44. Opposite sides of a crushed triangular fruit, apex incomplete. × 20. (V.43829.)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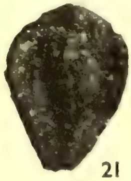
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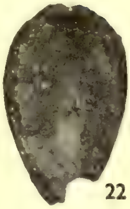
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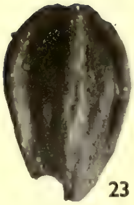
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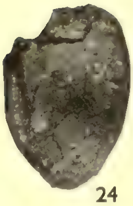
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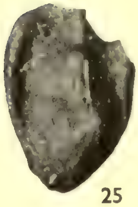
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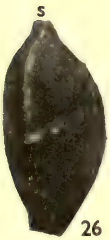

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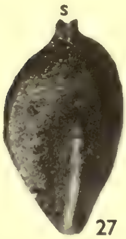

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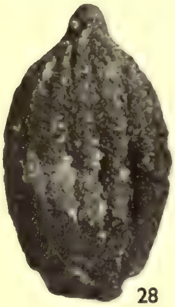
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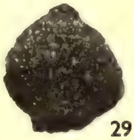
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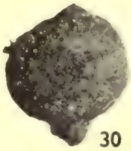
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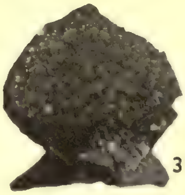
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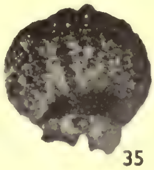
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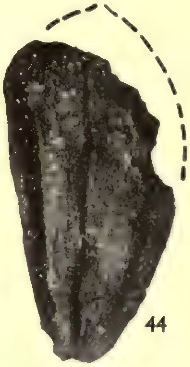
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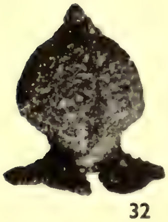
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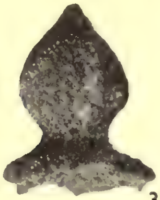
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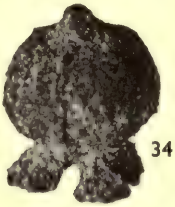
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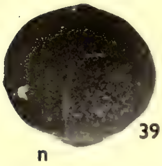

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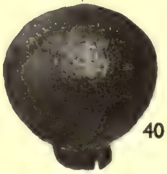
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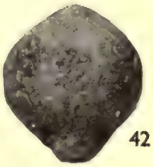
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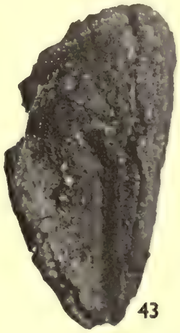
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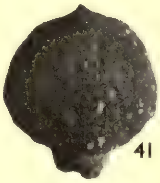
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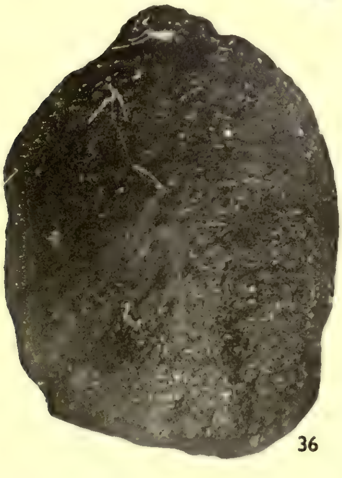
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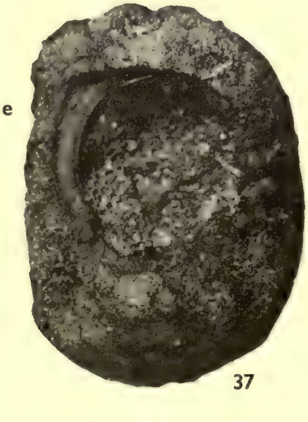

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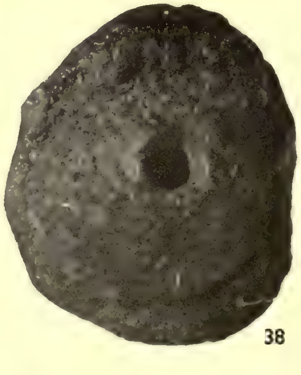
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PLATE 29

Myrica boveyana (Heer)

FIG. 45. Valve of endocarp, much abraded. × 9·5. (V.43832.)

FIG. 46. Same, inner side showing characteristic form of locule; stylar canal at apex; *v*, vascular canal. Note broad sutures. × 9·5.

FIG. 47. Better preserved fruit, exterior of valve (cut off on left by edge of plate). × 15·5. (V.43831.)

FIG. 48. Inner surface of one valve of the above, *st*, stylar canal; *v*, vascular canal. × 15·5.

Myrica ? *colwellensis* n.sp.

FIG. 49. Holotype. Endocarp, exterior, showing longitudinal furrows with fibres. × 15. (V.43834.)

FIG. 50. Valve of same, inner surface, showing typical locule and coarse cells of locule lining; *st*, stylar canal; *s*, crumpled seed; *v*, vascular canal. × 15.

FIG. 51. Second valve of same, exterior, bitten by insect (?), on right. × 15.

FIG. 52. Valve of endocarp, exterior, imperfect above. × 9·5. (V.43835.)

FIG. 53. Same, inner face; *v*, vascular canal. × 9·5.

FIG. 54. Valve of abraded endocarp, exterior. × 9·5. (V.43836.)

FIG. 55. Same, inner surface, *st*, stylar canal. (Cavity full of sand grains.) × 9·5.

Ficus lucidus Chandler

FIG. 56. Crushed endocarp, burst at *p* overlying placenta, × 20. (V.43838.)

Centrospermae. Family ? Genus ?

FIG. 57. Seed bursting at hilum. × 20. (V.43839.)

Brasenia ovula (Brongniart)

FIG. 58. Seed without embryotega, aperture for which is at *a*. × 15·5. (V.43841.)

FIG. 59. Smaller seed. × 15·5. (V.43840.) Both the above from south of Brambles Chine.

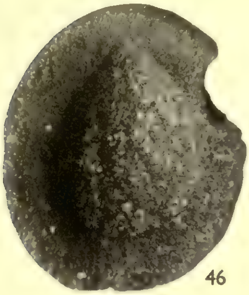
Nymphaea sp.

FIG. 60. Seed with embryotega, *e*. × 15. (V.43850.)

FIG. 61. Another, embryotega missing. × 15. (V.43851.)

Nymphaeaceae. Genus ? (? *Brasenia ovula*)

FIG. 62. Hilar end of dorsiventrally crushed seed with embryotega just below centre of figure showing micropyle surrounded by radially arranged cells. × 15. (V.43852.)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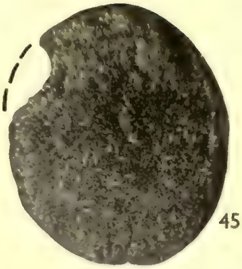
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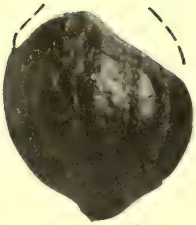
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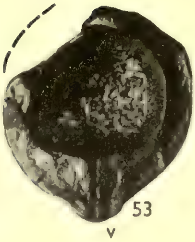

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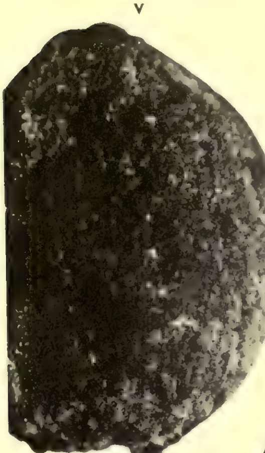

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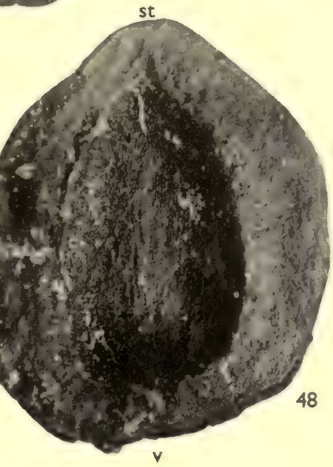

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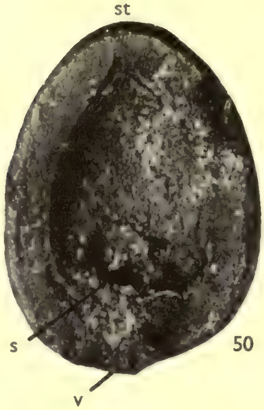

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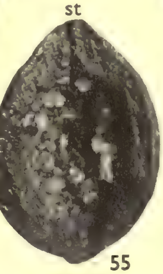

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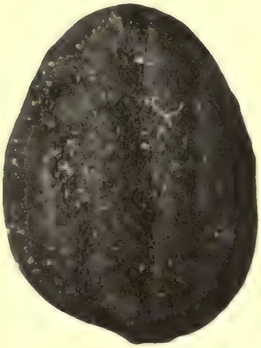
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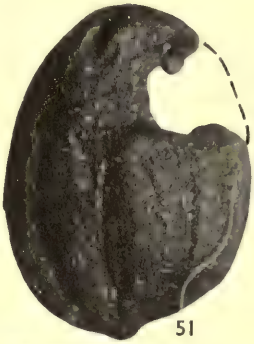
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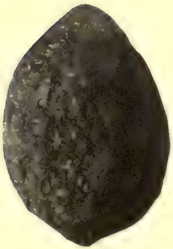
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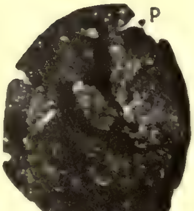

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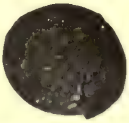
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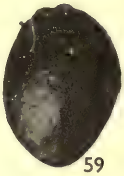
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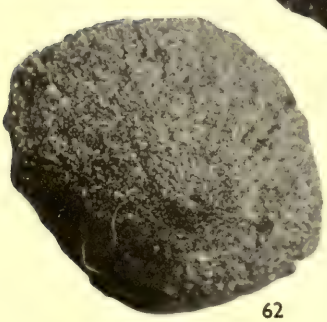
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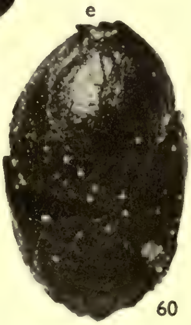

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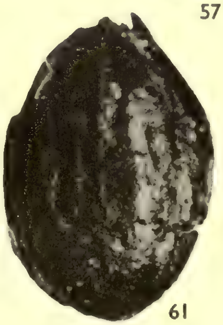
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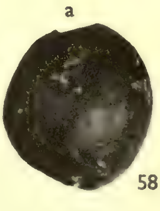

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PLATE 30

Brasenia spinosa Chandler

FIG. 63. Seed, tilted to show aperture for embryotega. × 15. (V.43844.)

FIG. 64. A seed, somewhat laterally compressed, apex showing aperture as in Fig. 63. × 15. (V.42121*a*.)

FIG. 65. Another tilted to show fine basal spines. × 15. (V.42121.)

FIG. 66. Apex of a seed with embryotega preserved showing small rimmed micropyle. × 15. (Decayed.)

FIG. 67. Smaller seed tilted to show embryotega at apex. Stout tubercles are seen. × 15. (V.20042*a*.)

FIG. 68. Another, side. × 15. (V.20041.)

FIG. 69. Another, tilted to show aperture for embryotega. × 15. (V.20041*b*.)

Figs. 64, 65, 67–69 from Lower Headon, Hordle for comparison. Figs. 64, 65 show seeds with slender spines. Figs. 67–69 are the variety with stout tubercles formerly separated as *Brasenia antiqua*.

Aldrovanda ovata (Chandler)

FIG. 70. Typical seed with long neck. × 15. (V.43853.)

FIG. 71. Another, bursting so as to show inner coat. × 15. (V.43854.) Below sewer pipe, Linstone Chine.

? *Rubus microspermus* C. & E. M. Reid

FIG. 72. Endocarp. × 20. (V.43859.)

FIG. 73. Another, abraded showing curved form. × 20. (V.43860.) Below sewer pipe, Linstone Chine.

Zanthoxylum hordwellense Chandler

FIG. 74. Seed, side. Long hilar scar at *h*. × 9. (V.43862.)

FIG. 75. Another, *h* as above. × 9. (Decayed.)

FIG. 76. Seed with more rounded outline. × 9. (V.43863.)

FIG. 77. Seed tilted to show hilar scar near right margin of figure. × 9·5. (V.43864.)

FIG. 78. More elongate seed tilted to show ventral margin with long narrow hilar scar in upper half. Hilar aperture in both at lower end of scar. × 9·5. (V.43865.)

FIG. 79. Same, side, hilar scar on left. *a*, position of hilar aperture. × 9.

FIG. 80. Seed in Fig. 77, side, hilar scar on right. × 9.

Hordwellia crassisperma (Chandler)

FIG. 81. Fruit, apex, with small subcircular perianth scar. × 20. (V.43868.)

FIG. 82. Seed, slightly broken at top of figure. Hilum at base. × 20. (V.43869.)

FIG. 83. Seed differently preserved in pyrites. × 20. (Decayed.)

FIG. 84. Somewhat crushed seed. × 20. (Decayed.)

FIG. 85. Typical larger seed. × 20. (V.43870.)

Decodon vectensis n.sp.

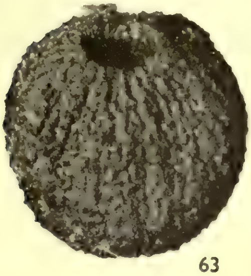
FIG. 86. Holotype. Seed, side, somewhat tilted to show valve on right beginning to gape at *v*. × 20. (V.43873.)

FIG. 87. Same, opposite side in true profile. Valve, *v*. × 20.

FIG. 88. Slender seed, valve, *v*, on left with concave outline. × 20. (V.43874.)

FIG. 89. Same, with valve on right, tilted so that it occupies half breadth of figure. × 20.

FIG. 90. Another, valve, *v*, gaping on right at base. × 20. (V.43875.)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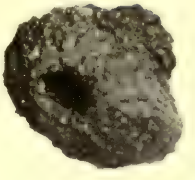
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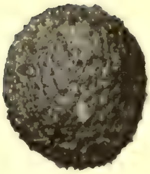
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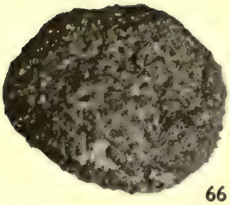
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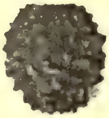
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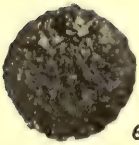
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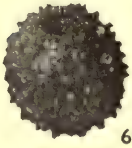
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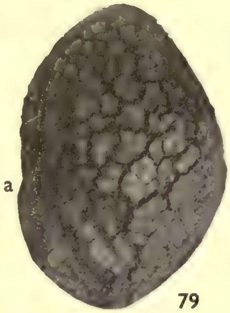

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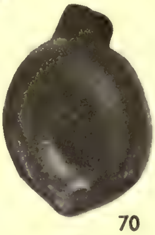
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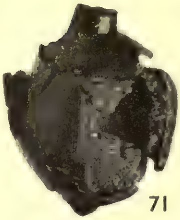
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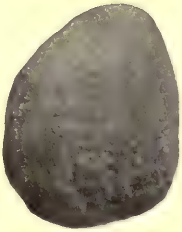
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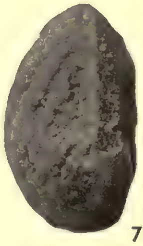
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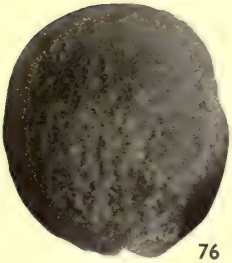
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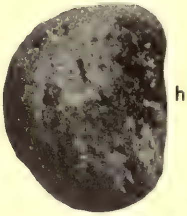

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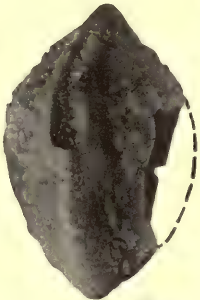
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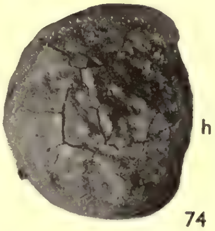

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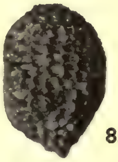
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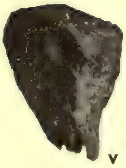

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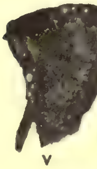

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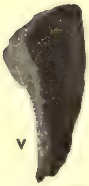

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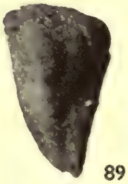
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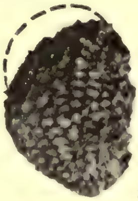
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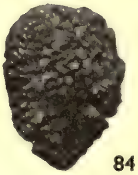
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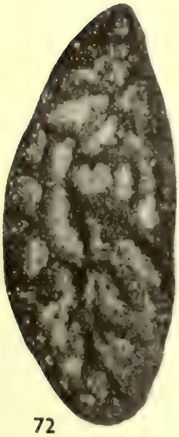
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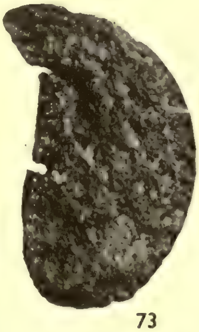
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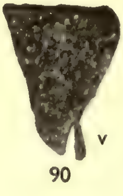

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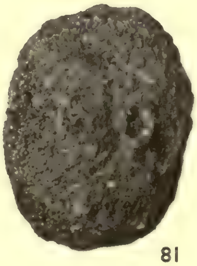
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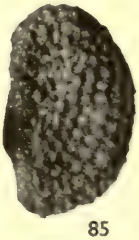
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PLATE 31

Decodon vectensis n.sp.

FIG. 91. Same seed as in Pl. 30, fig. 90. Valve on left. × 20.

FIG. 92. Seed with dorsal angle on right. × 20. (Decayed.)

FIG. 93. Ungerminated seed with closed valve on right. × 20. (V.43876.)

FIG. 94. Seed, ? abortive, looking onto slightly concave valve which extends almost to apex as shown by crack along its left margin. × 20. (V.43877.)

FIG. 95. Abortive seed. × 20. (Decayed.)

FIG. 96. Seed with cavity turned to left exposed by loss of valve. × 20. (V.43878.)

FIG. 97. Seed, edge of valve on left, dorsal angle forms outline on right. × 20. (V.43879.)

FIG. 98. Same, left edge is the dorsal angle, locule lies behind on right. × 20.

? *Microdiptera parva* Chandler

FIG. 99. Seed, dorsal, showing pitted germination valve in lower half. × 20. (V.43881.)

FIG. 100. Same, ventral, showing broad longitudinal seed-body carrying raphe ridge. × 20.

FIG. 101. Seed, dorsal, with longer valve. × 20. (V.43882.)

FIG. 102. Same, ventral. × 20.

FIG. 103. Subquadrangular seed, dorsal, valve partly hidden by distortion of specimen. × 20. (V.43883.)

FIG. 104. Same, ventral, showing broad seed-body flanked by depressions. × 20.

FIG. 105. Seed, dorsal, valve slightly swollen and cracked towards its apex. × 20. (V.43884.)

FIG. 106. Same, ventral, broad body clear. × 20.

FIG. 107. Seed, dorsal, seed-cavity, *c*, exposed by loss of valve. × 20. (Decayed.)

Sambucus colwellensis n.sp.

FIG. 108. Holotype. Seed, ventral. × 20. (V.43886.)

FIG. 109. Another, dorsal. × 20. (V.43887.)

FIG. 110. Seed, ventral, *h*, hilum. × 20. (V.43888.)

FIG. 111. Small seed, ventral, splitting marginally as in germination. × 20. (V.43889.)

FIG. 112. Seed, ventral, *h*, hilum. × 20. (V.34890.)

FIG. 113. Crushed seed, ventral, splitting as in Fig. 111. × 20. (V.43891.) Below sewer pipe, Linstone Chine.

Epacridicarpum headonense Chandler

FIG. 114. Fruit tilted to show apex with loculicidal splitting. × 20. (V.43894.)

FIG. 115. Another, side, showing flat apex, domed base. × 20. (V.43895.)

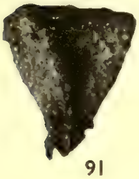
FIG. 116. Base of a fruit with median attachment scar. × 20. (V.43896.)

Epacridicarpum colwellense n.sp.

FIG. 117. Holotype. Fruit, apex, showing winged angles over locules alternating with concavities, *s*, over septa. × 20. (V.43898.)

FIG. 118. Another, base, somewhat distorted. × 20. (V.43899.)

FIG. 119. Another, basilateral view. Distorted. × 20. (V.43900.)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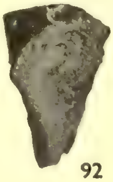
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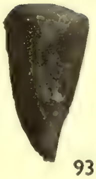
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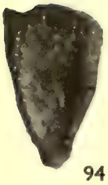
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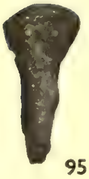
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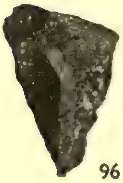
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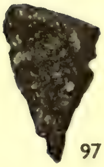
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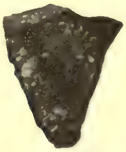
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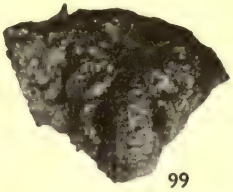
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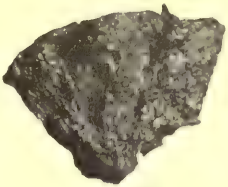
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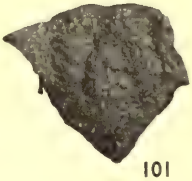
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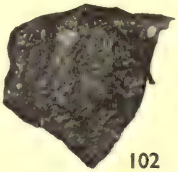
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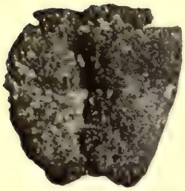
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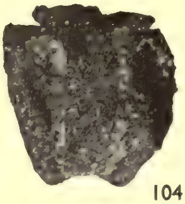
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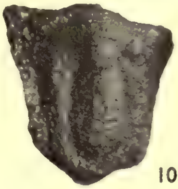
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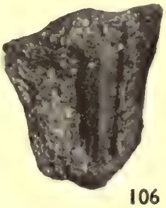
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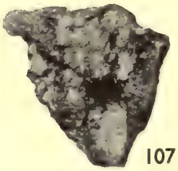

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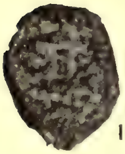
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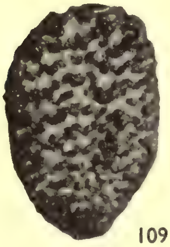
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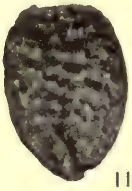

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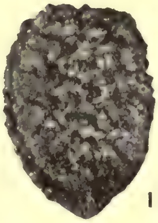

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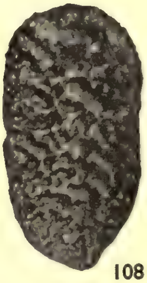
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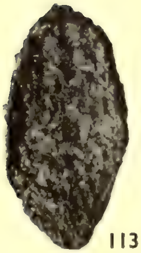
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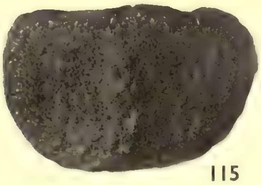
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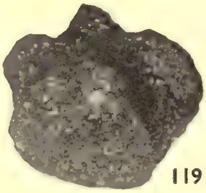
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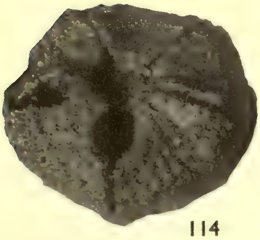
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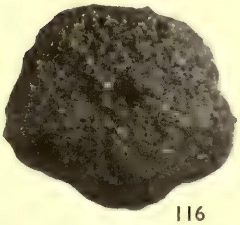
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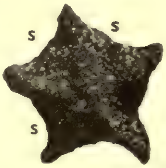

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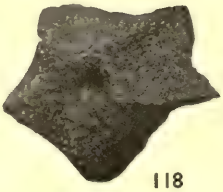
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PLATE 32

Carpolithus colwellensis n.sp.

FIG. 120. Holotype. Fruit showing tiny perianth segments, *p*; median angle with furrow, flanked by lateral facets. Faintly rippled surface due to fine tubercles seen on left. Base somewhat abraded. × 20. (V.43905.)

FIG. 121. Same, opposite flat surface. Two perianth segments clearly shown. × 20.

FIG. 122. Another, angled surface, median furrow filled by white matrix. Broken at apex so that locule is exposed at *l*. Excavated base complete. × 20. (V.43906.)

FIG. 123. Same, flat surface, base well shown. × 20.

FIG. 124. Smaller fruit, facetted surface. × 20. (V.43907.)

FIG. 125. Same, opposite flat surface. × 20.

FIG. 126. Another, imperfect at base, in longitudinal section. × 20. (V.43908.)

Carpolithus spp.

FIG. 127. Valve of ? capsule, bearing subterminal spine. × 9. (V.43909.)

FIG. 128. Same, opposite, internal, surface. × 9.

FIG. 129. Another, exterior, split below and somewhat collapsed. × 9·5. (V.43910.)

FIG. 130. Same, opposite side with ? ruptured septum. × 9·5.

FIG. 131. Small ovoid seed. × 20. (V.43912.)

FIG. 132. Similar but more elongate specimen. × 20. (V.43913.)

FIG. 133. Abraded fruit or seed with scar truncating apex. × 20. (V.43914.)

Unknown leaf

FIG. 134. Lobed or segmented leaf or pinnule fragment, upper surface. × 20. (Decayed.)

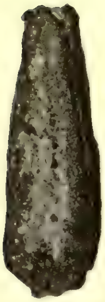
FIG. 135. Same, lower surface, showing broad convex midrib delimited by furrows. × 20.

FIG. 136. Three lobes of a larger specimen, upper surface. × 20. (V.43917.)

FIG. 137. Same, lower surface, showing broad midrib flanked by hollows partly concealed by recurved margins of lobes. (White patch a sand grain.) × 20.

FIG. 138. Fragment near base of leaf with lobes diminishing in size downwards. Upper surface. × 20. (V.43916.)

FIG. 139. Same, lower surface, showing conspicuous convex midrib. × 20.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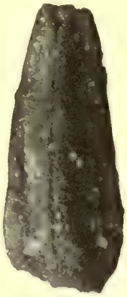
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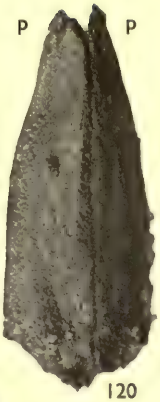

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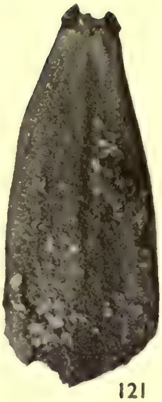
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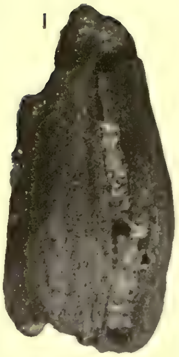

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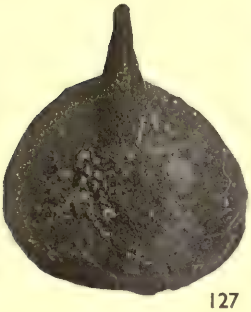
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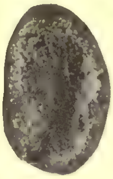
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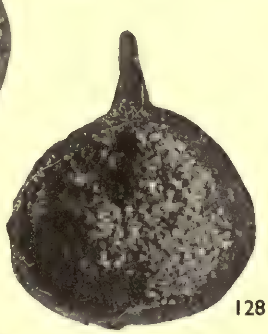
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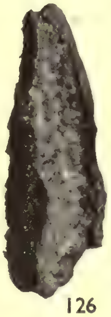
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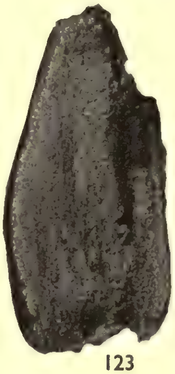
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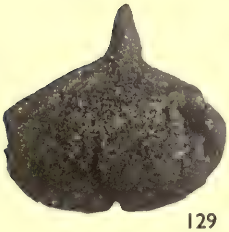
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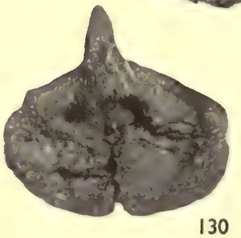
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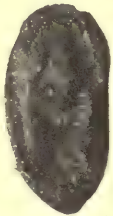
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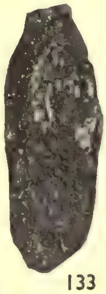
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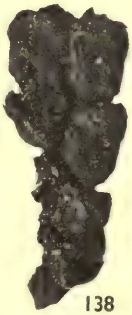
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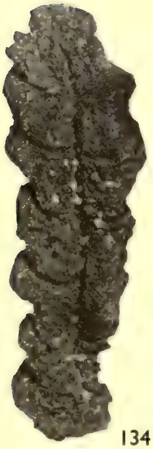
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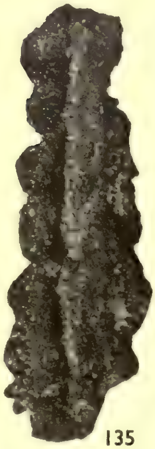
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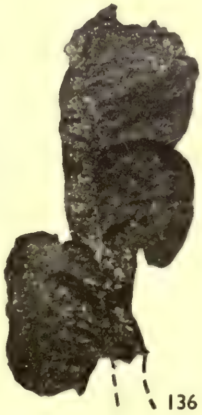
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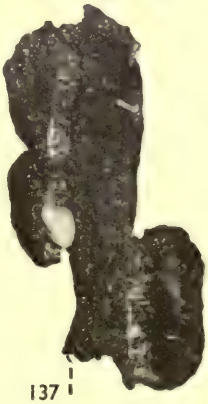
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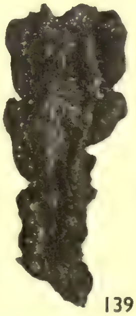
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PLATE 33

Carpolithus sp.

Fig. 140. Fruit showing cavity exposed by partial splitting into two valves, one now incomplete. *a*, attachment scar. × 14. (V.43915.)

Fig. 141. Same, opposite side, with obscure ribbing. Broken valve projects at *v*. × 14.

Figs. 142–147 from Osborne Beds, Isle of Wight.

Acrostichum lanzaeanum (Visiani)

Fig. 142. Fragment of pinnule showing characteristic nervation. cf. Text-fig. 3. × 2·5. No. 377 Geological Survey Museum from Cliff End near Colwell Bay.

? *Stratiotes neglectus* Chandler

Figs. 143–146. Seeds or valves, small, crushed, probably abortive. Figs. 143–145 external surface. Fig. 146 internal surface. Figs. 144, 146 have the keel partly broken at *b* along the line of the raphe. *h*, position of hilum. × 6. (V.43923–26.)
From Osborne.

Dicotylophyllum pinnatifidum Reid & Chandler

Fig. 147. Terminal fragment of leaf. × 6 approx. No. 376 Geological Survey Museum, from Cliff End, Colwell Bay.

Figs. 148–165 from Bembridge Beds, Isle of Wight except Fig. 153 from Hamstead Beds for comparison.

? *Potamogeton* sp.

Fig. 148. Impression of upper surface of tuft of leaves still attached to stem. Crushed so as to give appearance of a whorl. × 1. (V.23428.)

Fig. 149. Part of leaf at *x* in Fig. 148 showing toothed margin at *m* and series of nerves and bast bundles. × 3. From Insect Limestone, Thorness Bay.

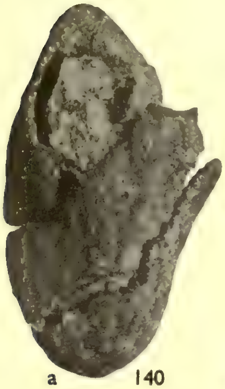
Limnocarpus forbesi (Heer)

Fig. 150. Endocarp, side, keel on right, *s*, style. Large lateral foramen, *l*, filled with matrix. Crushed but surface rugosities well preserved. × 15. (V.43930.)

Fig. 151. Another, dorsilateral view, showing ridged keel. Style broken. × 15. (V.43931.)

Fig. 152. Another, crushed and tilted to show tip of ridged keel. × 15. (V.43932.)
Marls below Chapel Corner, Wootton.

Fig. 153. Similar crushed endocarp for comparison with Fig. 151. Style broken. × 15. (V.43960.) Waterlily Bed of Hamstead Beds, Hamstead cliff.



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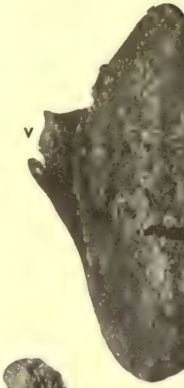

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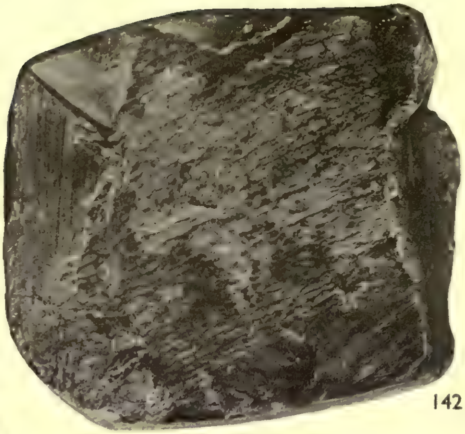

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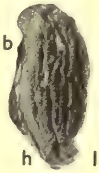

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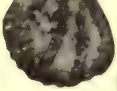

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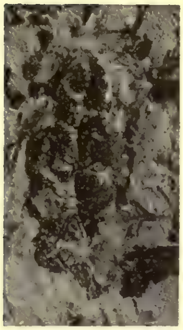

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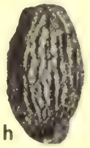

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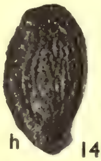

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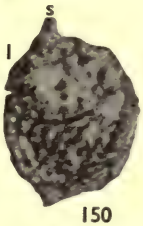

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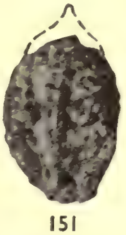

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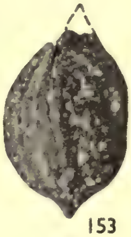

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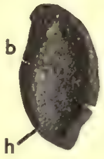

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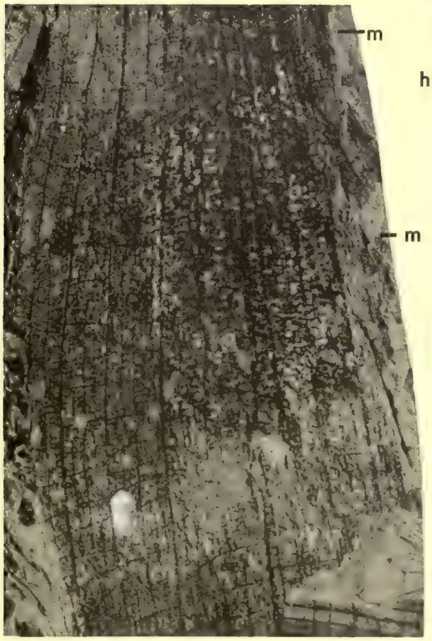

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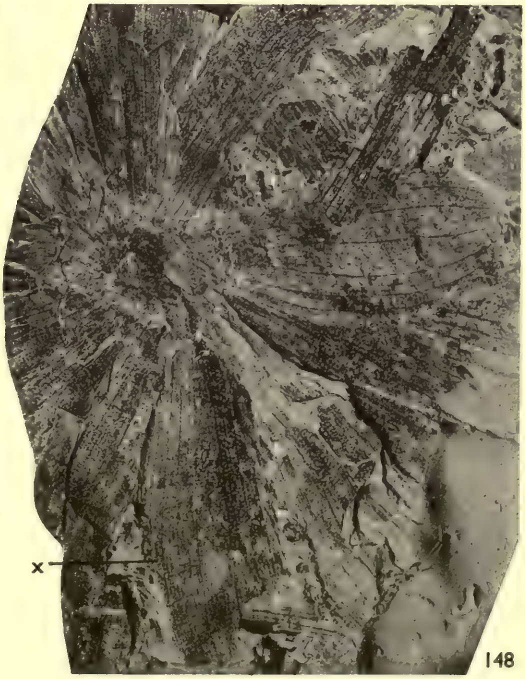

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PLATE 34

Stratiotes neglectus Chandler

FIG. 154. Valve, exterior, typical seed. × 6·5. (V.40079.)

FIG. 155. Same, interior, showing diagonal raphe crossing keel on left. *m*, micropyle. × 6·5. Marls, Hamstead Ledge.

Celtis edwardsi n.sp.

FIG. 156. Holotype. Endocarp, side, showing reticulate surface. Margin lies in plane of symmetry. *a*, one of a pair of apical depressions. × 6·5. (V.43919.)

FIG. 157. Same at right angles to the above ; *a,a*, apical depressions (part of system of reticulations. × 6·5.

FIG. 158. Same, apex, plane of symmetry vertical. Pair of depressions seen just above equator of figure. × 6·5.

FIG. 159. Same, base, plane of symmetry vertical. × 6·5.

FIG. 160. Internal cast of another endocarp (virtually equals seed) viewed at right angles to plane of symmetry, *p*, placenta. × 6·5. (V.43920.) Bembridge Limestone, Headon Hill.

Ranunculus ovaliformis (Reid & Chandler)

FIG. 161. Impression of achene with large recurved style, basal attachment and impressions of small tubercles in central area. × 6·5. (V.23429.) Insect Limestone, Thorness Bay.

Carpolithus sp.

FIG. 162. Valve of fruit or endocarp showing apical style, *s*, and basilateral flanges. × 4.

FIG. 163. Same, inner surface, showing basal canals and coarse network of fibres impressed on cavity wall. Also smooth marginal suture. × 5·5.

FIG. 164. Exterior of another specimen. × 4.

FIG. 165. Same, opposite side with near valve broken so that cavity and basal canal are shown. × 4. From marly pocket in Bembridge Limestone, Sticelett Ledge, Isle of Wight. All in Sandown Museum, J. F. Jackson Coll.

Figs. 166–204 from Hamstead Beds, Isle of Wight.

Typha latissima Al. Braun

FIGS. 166–170. Five seeds truncated above by micropylar disc with central mucro, pointed chalazal end at base. × 15. (V.43940–44.) " Waterlily Bed ", Hamstead.

? *Sparganium multiloculare* Reid & Chandler

FIG. 171. Endocarp, side. × 15. (V.43947.)

Sparganium sp.

FIG. 172. Endocarp, apex, showing aperture of stylar canal leading into locule. × 6·5. (V.43948.)
" White Band ", Bouldnor cliff.

Potamogeton tenuicarpus C. & E. M. Reid

FIGS. 173–176. Four endocarps, *v*, valve. × 15. V.43949–50 from " Waterlily Bed ", Hamstead. V.43954–55 from same at Bouldnor cliff.

Limnocarpus forbesi (Heer)

FIG. 177. Uncrushed pyritized endocarp. × 12. (Decayed.) Hamstead Beds, Hamstead cliff.

FIG. 178. Another, side. *s*, stalk ; *st*, style ; keel on right. × 15. (V.43957.) " Waterlily Bed ", Hamstead cliff.

? *Caricoidea minima* (Chandler)

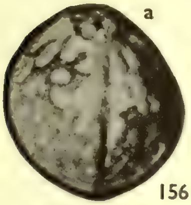
FIGS. 179–180. Two endocarps. Fig. 180 shows lateral ridge and basal flange. × 12. (V.43965–66.) Hamstead cliff.

Stratiotes neglectus Chandler

FIG. 181. Seed, exterior. × 6·5. (V.43968.)

FIG. 182. Valve of seed, interior. × 6·5. (V.43969.)

In beds full of *Potamaclis turritissima* Hamstead cliff, said to come from the Hamstead Series.



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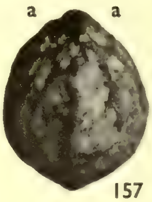

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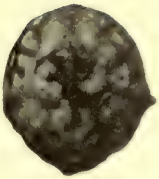

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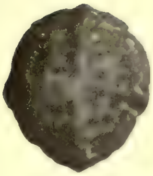

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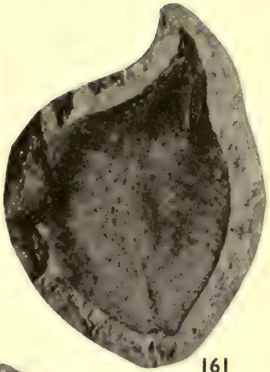

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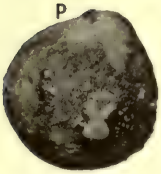

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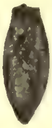

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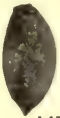

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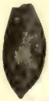

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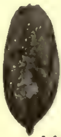

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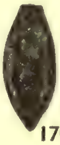

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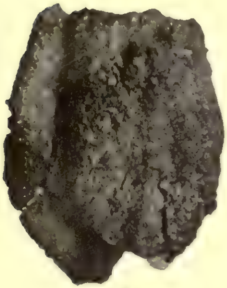

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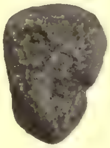

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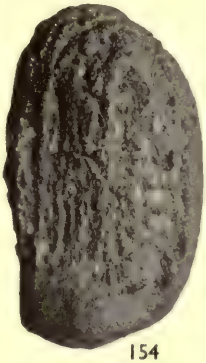

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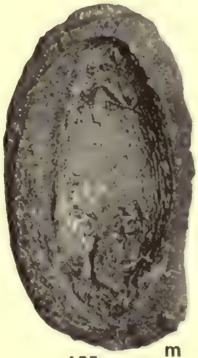

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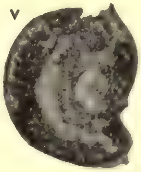

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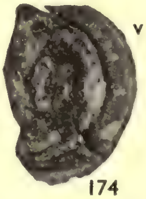

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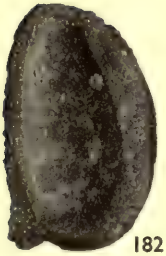

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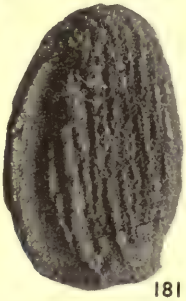

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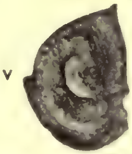

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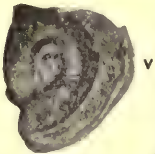

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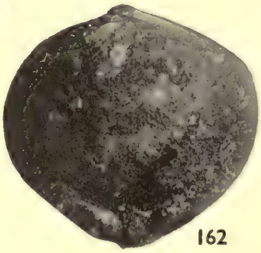

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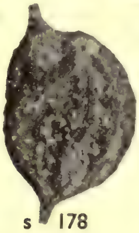

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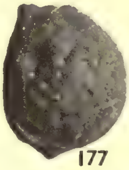

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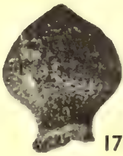

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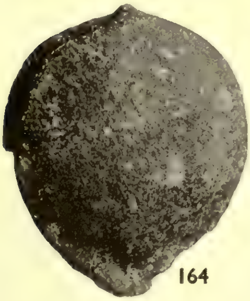

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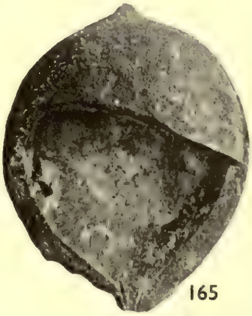

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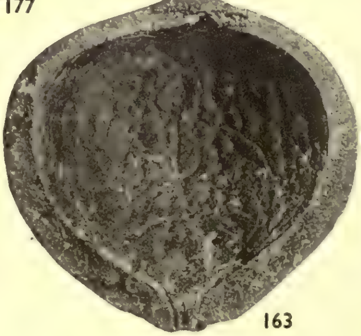

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PLATE 35

Stratiotes websteri (Brongniart)

FIG. 183. Typical valve of seed, exterior. Keel on left. Collar, *c*. × 6. (V.43976.)

FIG. 184. Another, inner surface, showing short transverse raphe. ***h***, hilum ; ***m***, microyple. × 6. (V.40072.)

FIG. 185. Narrower small seed. Lettering as above. × 6. (V.43974.)

FIG. 186. Relatively unabraded seed. Keel on right. × 6. (V.43975.) Hamstead cliff.

Stratiotes acuticostatus Chandler

FIG. 187. Holotype. Seed, exterior, showing sharp interrupted ridges ; ***k***, broad keel. Note coarse pitting. × 6. (V.40075.)

FIG. 188. Valve of another, inner surface, showing conspicuous raphe traversing keel on left; *m*, micropyle. × 6. (V.40074.)

FIG. 189. Long narrow seed, exterior, with typical crested ridges. × 6. (V.44653.)

FIGS. 190–192. Three small seeds, ? immature. Figs. 190, 191 show exterior, fig. 192 interior. × 6·5. (V.44174, V.44176, V.44179.)
Bouldnor cliff.

Sabal major (Unger)

FIG. 193. Impression of central part of a leaf with scanty carbonaceous remains. Shows tapering rachis and asymmetry at top of petiole. × 0·66. Middle Hamstead Beds, Hamstead. Sedgwick Museum, Cambridge, H. Keeping Coll.

Brasenia ovula (Brongniart)

FIG. 194. Crushed seed with embryotega, ***e***. × 12. (V.44185.) Hamstead cliff.

Leguminosae. Genus ?

FIG. 195. Much crushed seed. × 12. (V.44192.) Hamstead cliff.

Aldrovanda intermedia Reid & Chandler

FIG. 196. Seed looking onto raphe ridge. × 15. (V.44193.) Hamstead cliff.

? *Ilex* sp.

FIG. 197. Dorsiventrally flattened endocarp. Scar of attachment median near base. × 12. (V.44194.) Hamstead cliff.

Carpolithus sp. (*Spirematospermum* sp. ?)

FIG. 198. Part of pod ; *s*, stalk ? White infilling lies within locule and is exposed where carpel wall has broken away. × 1. (41424.) Lower Hempstead Marls, Hempstead.

Carpolithus spp.

FIG. 199. Crushed seed, possibly peculiarly preserved *Brasenia* with aperture for an embryotega at *e*. × 15. (V.44187.) Hamstead cliff.

FIG. 200. Crushed seed with basal scar. × 12. (V.44200.) Hamstead cliff.

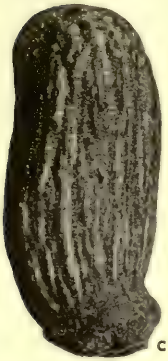
FIGS. 201–204. Translucent tegmens of unidentified seed ? with conspicuous scar (chalaza ?) at one end. Two have split longitudinally at opposite end (Figs. 203, 204) perhaps as result of crushing. × 15. (V.44201–03, Fig. 201 decayed.) "Waterlily Bed", Hamstead cliff.

FIGS. 205, 206. F. E. Edwards Collection Headon Hill in ironstone nodule ? Horizon ? possibly Lower or Upper Headon.

Stizocarya sp.

FIG. 205. Valve of endocarp, exterior. × 3. (V.43928.)

FIG. 206. Same, inner surface, showing apical part of funicular canal traversing wall to subapical placenta. Canal abraded below *f*. × 3.



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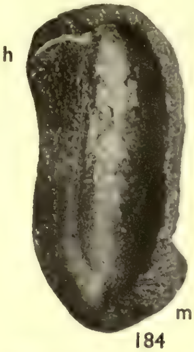

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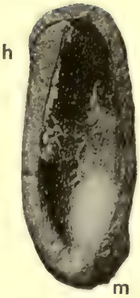

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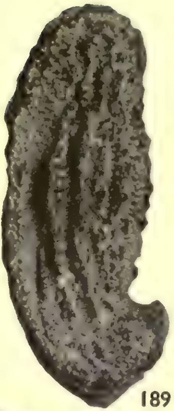

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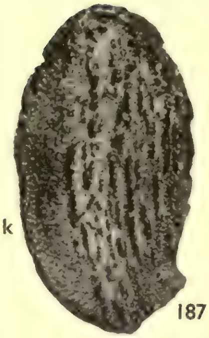

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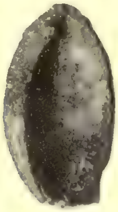

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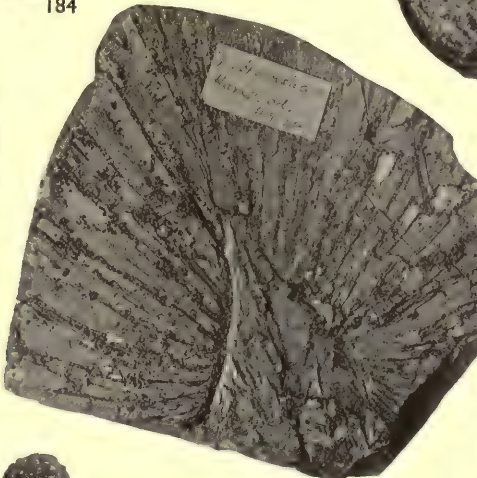

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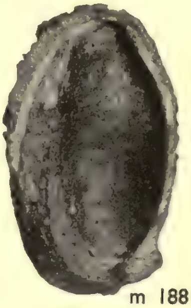

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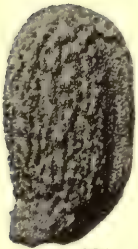

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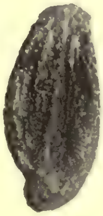

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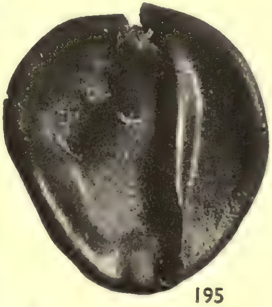

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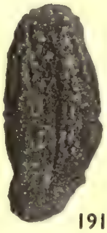

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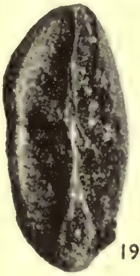

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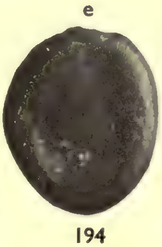

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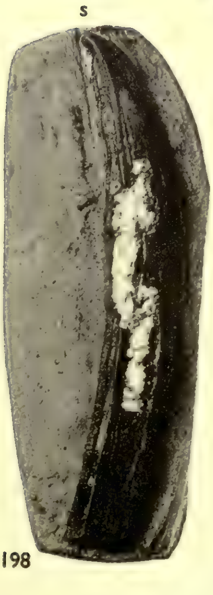

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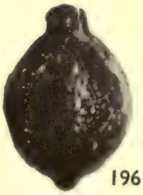

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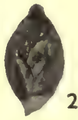

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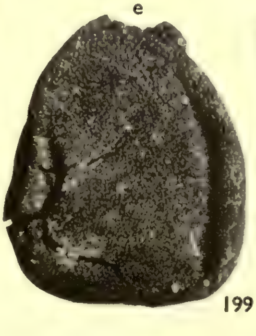

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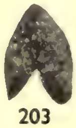

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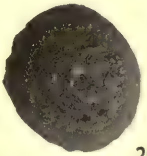

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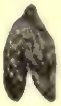

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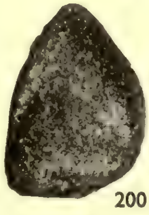

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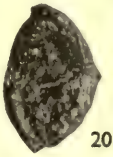

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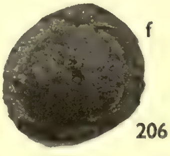

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